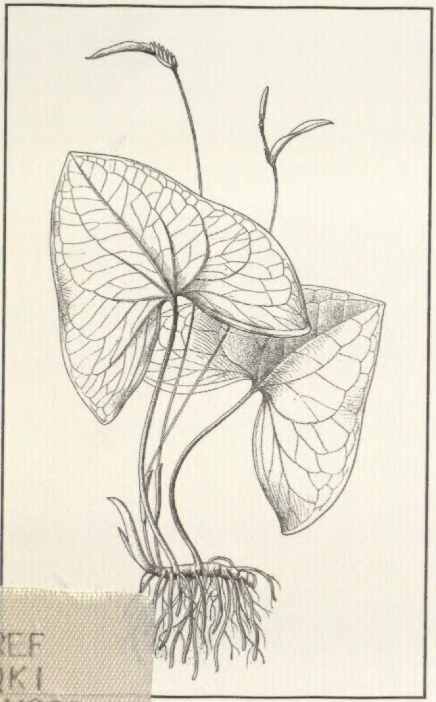
Comparative External Pollen Ultrastructure of the Araceae and Putatively Related Taxa

Michael H. Grayum



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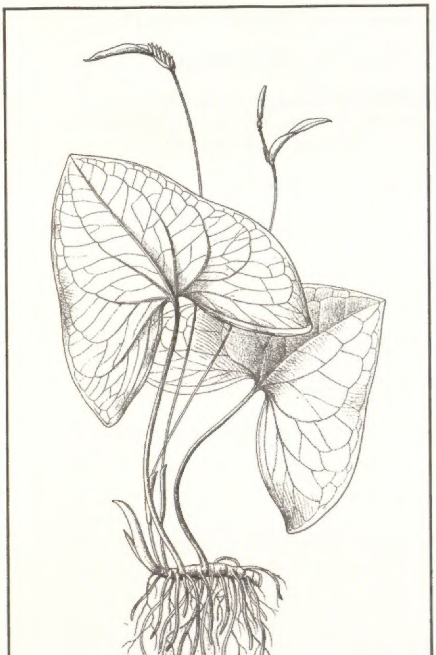

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CONTENTS

COMPARATIVE EXTERNAL POLLEN ULTRASTRUCTURE OF THE ARACEAE AND PUTATIVELY RELATED TAXA

Michael H. Grayum[1]

ABSTRACT

An extensive survey of external pollen morphology in the monocot family Araceae was undertaken, using both light and scanning electron microscopy. Pollen of approximately 380 species was examined, representing 99 of the 105 currently recognized genera and 98 of the 114 accepted sections and subgenera. The data collected were analyzed to determine polarities for the character states of each major pollen character. The most primitive pollen in Araceae is regarded as monosulcate, boat-shaped, heteropolar, bilaterally symmetrical and small to medium-sized (22–34 μm in diameter). It is shed in monads, has foveolate to reticulate exine sculpturing, and is probably tectate-columellate. Inaperturate, boat-shaped pollen evidently represents a common intermediate evolutionary stage. The major implications for internal aroid taxonomy emerging directly from considerations of pollen morphology are summarized. The relationship of the Araceae to other families is briefly considered, based in part on a limited SEM study of pollen of pertinent outgroups. The Araceae are in general considered more closely related to the Alismatiflorae than the Areciflorae, Typhales, or Piperales. The Lemnaceae are not closely related to *Pistia*, and their relationship to the Araceae in general needs to be reassessed.

INTRODUCTION

The Araceae are a mainly tropical family of herbs and vines comprising about 105 genera and over 2,500 species. The family has universally been placed within the subclass Monocotyledoneae, or Liliopsida (i.e., the monocots); however, its relationship to the other members of that taxon is not well understood, and some authors have even suggested a connection with certain dicotyledonous families.

The genera of the Araceae are highly diverse with respect to growth habit, leaf morphology, flower morphology, and most other character fields that have been investigated. They have been grouped together mainly on the basis of the distinctive inflorescence: a spadix of tiny flowers, which is virtually always subtended by a solitary spathe. As one would anticipate, the Araceae are united by a number of other less readily observable features, such as: the presence of raphides; a superior ovary with bitegmic, usually tenuinucellate ovules with a nucellar cap; a haustorial endosperm with an allegedly cellular type of development; an endothelium; amoeboid anther tapetum; successive pollen mother-cell cytokinesis; vessels mostly confined to the roots; broad leaves; berrylike fruits; and the presence of leucoanthocyanidins (Hegnauer, 1963; Cronquist, 1981). The above characteristics, however, are not uniformly present in every aroid genus; moreover, there are other, presumably derived character states—presence of laticifers, presence of trichosclereids, unisexual and/or naked flowers, reticulate leaf venation, presence of tyrosin-derived cyanogenic compounds—that characterize various subgroups within the family.

A thorough understanding of all characters of putative phylogenetic importance is essential to any attempt to elucidate the evolutionary history of any natural group of organisms. It has been a major task of this study to analyze the polarity and distribution of character states of the various pollen characters both within Araceae and in appropriate outgroups (suggested relatives), in an effort to deduce a tenable phylogeny for the family (see Grayum, 1990) and to shed light on its position in the phylogenetic scheme of the angiosperms.

The original data presented in this work include an across-the-board survey of pollen exine sculpturing for the family Araceae, using scanning electron microscopy (SEM). A comprehensive atlas of aroid pollen, photographed under light microscopy, is already available (Thanikaimoni, 1969), which accurately portrays aperture types within the family and conveys a myopic impression of great di-

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versity in exine sculpturing. This work has been an extremely useful reference throughout the present investigations; however, the advent of SEM has revolutionized systematically oriented palynological studies to such an extent (see, e.g., Walker & Doyle, 1975; Lewis, 1977) that the present study is warranted.

Scattered SEM micrographs of many aroid genera have already been published; however, no full-scale investigation of araceous pollen at the SEM level has yet been undertaken. Indeed, although a TEM section through the aperture of an unidentified *Anthurium* species had appeared in the literature three years prior to the publication of Thanikaimoni's study (Gullvåg, 1966), the first SEM micrograph of an araceous pollen grain known to me—of the obscure Malagasy species *Carlephyton glaucophyllum*—did not appear until three years afterward (Bogner, 1972).

The value of pollen exine sculpturing, as observed under SEM, has already been demonstrated as an indicator of phylogenetic relationships by numerous studies (e.g., Nowicke & Skvarla, 1979; Walker & Walker, 1981; and others), and SEM photos of pollen are now routinely included in taxonomic monographs and even species descriptions. Frequently, SEM is combined with transmission electron microscopy (TEM), which is employed to study exine stratification. This technique has not been exploited during the present study, for various reasons, chiefly time limitations. It was felt that the likelihood was slim that any worker would attempt such an extensive survey of pollen morphology in a family this size using both SEM and TEM and that, confronted by such an intimidating task, palynologists would tend to chip away at the family genus by genus, so that the whole picture might be very long in emerging. Since TEM work on araceous pollen was already underway in a European laboratory (G. Thanikaimoni & D. Lobreau-Callen, in litt.), it was decided to direct all efforts toward SEM. Although much can be learned from exine sculpturing alone, the perspective provided by TEM sectioning is essential for interpreting exine stratification, and the results of these studies are eagerly awaited. Meanwhile, it is expected that the scanning electron micrographs and descriptions presented here will serve as valuable guides for those workers.

Other important pollen characters—size, shape, and aperture type—were validated in the present study using light microscopy.

The survey of pollen has been further extended to include certain species in selected outgroups. This was done mainly to facilitate the polarization of pollen character states within Araceae by broadening the data base for appropriate outgroups. However, this research has enabled certain insights relevant to the outgroups themselves.

Inasmuch as methodologies designed to infer the course of evolution (such as cladistic analysis) rely upon the preexistence of adequate character inventories, every effort was made during the present survey to achieve the broadest scope possible, taxonomically and geographically. Material was sought from every section (naturally, without complete success), and, within a given genus or section, from species in disjunct portions of the range. The breadth of this study is such that our knowledge of the distribution of major pollen character states in the Araceae may now be said to be on a par with that of many floral features. This information, considered against a backdrop of the distribution and putative polarities of character-states already known from other character-fields (Grayum, 1990) and with reference to the fossil pollen record, was used via the process of "reciprocal illumination" (Hennig, 1966) to assign polarities to the pollen character states. This information has been employed to formulate what is here envisioned as the most plausible phylogenetic scheme for the various genera of Araceae (Grayum, 1990) and, via outgroup analysis (see, e.g., Wiley, 1980), to indicate which of several purported "nearest relatives" (if any) is the best candidate.

ACKNOWLEDGMENTS

This work was submitted as part of the requirement for a Ph.D. degree at the University of Massachusetts. I am deeply indebted to James W. Walker, advisor of my graduate studies, who suggested this project and provided the optimal amount of support, encouragement, and involvement throughout its course. Dr. Walker placed his extensive collections of araceous pollen at my disposal and made many additional collections solely for the purposes of this research. I owe a similar debt of gratitude to Audrey G. Walker, whose meticulous and expert instruction in all technical aspects of this undertaking, including pollen isolation, SEM microscopy, and darkroom work, contributed to an invaluable apprenticeship.

I am also grateful to the other members of my dissertation committee, K. S. Bawa, Margaret E. Bigelow, and David L. Mulcahy, for their critical reading of the manuscript.

Most members of the international aroid community contributed to this project in one way or another. I especially thank Josef Bogner of the

Munich Botanical Garden (M), who supplied the majority of fresh pollen samples as well as stimulating discussion and a steady flow of reprints. Without his unique combination of taxonomic expertise and horticultural proficiency, the inventory of araceous pollen would have been far less comprehensive.

Substantial quantities of fresh or dried pollen samples, as well as valuable communication, were also provided by the following individuals: Thomas B. Croat, Missouri Botanical Garden (MO); Barry E. Hammel, Missouri Botanical Garden; Michael Madison, formerly of The Marie Selby Botanical Gardens (SEL); Simon Mayo, Royal Botanic Gardens, Kew (K); and Dan H. Nicolson, United States National Herbarium (US). Elias Landolt of Zürich (RUEB) graciously provided most of the flowering material of the Lemnaceae. I am grateful to all of these workers.

The following individuals supplied additional pollen samples: James H. Beach (MASS); Albert J. Bednarick (BH); Paul Chai (SAR); Ruth Henderson, Gloucestershire, England; Li Hen (KUN); Jan Muller (L); Karel Rataj (SUM); Thomas Raus (B); Benjamin C. Stone, Kuala Lumpur, Malaysia; Barbara M. Thiers (NY); and P. B. Tomlinson, Petersham, Massachusetts.

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PART 1. EXTERNAL POLLEN MORPHOLOGY OF THE ARACEAE

During the present investigation, pollen from 380 species of Araceae representing 99 of the 105 currently accepted genera (Bogner & Nicolson, 1991) was studied. Of *Bucephalandra*, *Heteroaridarum*, and *Helicodiceros*, only inadequate and/or dubious material was available. Good material of *Aglaodorum* was procured too late for examination under SEM. No samples of *Mangonia*, *Gearum*, or *Zomicarpella* were obtained. With contributions from other sources, however, good pollen data are now available for every aroid genus except *Heteroaridarum*. At the infrageneric level, pollen from 98 of the 114 currently accepted sections and subgenera (according to the taxonomic references cited for each genus) has been examined.

MATERIALS AND METHODS

Spadices or portions thereof, excised flowers, stamens or anthers, or more or less pure pollen, depending on the species and the circumstances, were collected from live material or herbarium sheets (or very rarely from spirit collections). The United States National Herbarium (US) and the Royal Botanic Gardens, Kew (K), provided the bulk of the samples from herbarium sheets; supplemental material was obtained from a range of other sources.

Each sample, regardless of the form and source, was treated the same way, as follows: the pollen was first extracted and rehydrated by boiling in water to which a drop of Photo-Flo 200 solution (Eastman Kodak Co., Rochester, New York) had been added, then subjected to one minute of sonication to shake additional pollen grains loose and help remove any pollenkitt. If these procedures yielded no pollen, anthers were mashed lightly with a glass rod; it was discovered, however, that in Araceae, unlike some other families, good pollen is very rarely recoverable via mashing if boiling and sonication have failed.

The pollen (with accompanying water) was then removed to a centrifuge tube via micropipetting, run up to 75% acetone and resonicated, then taken back to 100% water and washed several times. Following this, more or less pure pollen was isolated via vacuum filtration onto a UniPore Polycarbonate Membrane (Bio-Rad Laboratories, Richmond, California) and covered with another such membrane, the whole unit being sandwiched between two disks of filter paper and snapped into a flow-through, ring-locking holder fashioned from the end of a Beem capsule (Ernest E. Fullam, Inc., Schenectady, New York). Each sample, thus secured, was stored in 100% acetone to await critical-point drying.

Samples were critical-point dried (Lynch &

Webster, 1975) in acetone, approximately 15 at a time, using a Sorvall Critical Point Drying System (Newtown, Connecticut), then mounted individually on copper stubs and sputter-coated (Damblon, 1975) with gold/palladium for 4½ minutes on a Polaron SEM Coating Unit E5100 (Polaron Instruments Inc., Hatfield, Pennsylvania) using argon.

All material was studied and photographed on a JSM-35 Scanning Microscope (JEOL Ltd., Tokyo, Japan) at 30 kv. The selected results of this photographic survey of aroid pollen appear in Figures 1–397. Low-magnification (whole grain) shots were taken at various magnifications, as indicated in the figure captions. High-magnification (detail) shots were uniformly taken at ×12,000, with just two exceptions (Figs. 218, 302).

Permanent light slides were prepared for all samples, except where material was so limited that all was required for SEM work. Each sample was centrifuged in acetone and acetolyzed (Erdtman, 1960) overnight at 65°C in a 9 : 1 mixture of acetic anhydride : sulfuric acid, then mounted in glycerine jelly. The light slides were used to study aperture features observable only via transmitted light, as well as pollen shape and size.

Pollen size was calculated for each sample based on measurements of ten grains, except where this many could not be located. The longest dimension was measured in every case, in micrometers (μm). If more than one sample (or subspecies) was available for a given species, the means for each sample (or subspecies) were pooled to arrive at a single figure for the species. The mean pollen size for each genus is thus based on the number of species investigated rather than the number of samples. Size ranges given for each genus represent the range of species means, rather than the absolute ranges. Thus ranges are not provided for monotypic genera or genera for which pollen of only one species was measured, unless more than one sample was studied.

Two aroid genera bear pollen in permanent tetrads; the mean size of tetrads as well as individual grains was determined for these genera. For a few genera, no good light slides were produced (or else meaningful measurements were impossible due to distortion of thin-walled grains by sonication and/or acetolysis), hence pollen size was calculated directly from the SEM micrographs; these measurements are indicated by an asterisk (*) in the pollen descriptions.

Formal pollen descriptions are provided in the following section for all genera investigated. Information on aperture type, polarity, pollen shape, symmetry, pollen-unit, pollen size, and exine sculpturing is presented using the terminology of Walker & Doyle (1975). Apparent rather than absolute pollen grain symmetry (Walker & Doyle, 1975) is indicated in the case of nonradiosymmetric grains, inasmuch as aroid pollen grains were seldom observed in tetrads. Existing terminology for exine sculpturing was developed mainly on the basis of light microscopic studies, and is often inadequate to describe variation observable at the SEM level (Hideux & Ferguson, 1976). For this reason, descriptive phraseology has been freely coined as needed; although an effort has been made to use familiar terms, the reader is referred to the plates for clarification wherever necessary. The term "verruculate" has been used here to cover various kinds of fine and usually irregular roughenings of the exine surface, i.e., much in the way the term "scabrate" has generally been used by light microscopists. "Scabrate" is here used more specifically, i.e., for more discrete, evenly distributed, and granular roughenings (see, e.g., Fig. 247).

Previously published SEM and TEM micrographs of araceous pollen have been cited insofar as the author is aware of them. Light micrographs of pollen of most araceous genera can be found in the comprehensive work of Thanikaimoni (1969).

For each genus, the number of species examined is indicated, out of the total number attributed to the genus. The latter represent the estimates of Croat (1988), except where superseded. Comparable data are provided for sections and/or subgenera, where present, according to the taxonomic reference(s) cited for each genus.

Some of the more significant data from the pollen descriptions are presented in a much abbreviated form in Table 1, following the plates. This table also provides an index to the generic descriptions.

The pollen descriptions, as well as the plates and Table 2, are arranged in a linear order more or less approximating the phylogeny proposed in Grayum (1990). The correspondence is unfortunately not exact, since the descriptions and plates had to be prepared before the phylogeny could be finalized. (The arrangement of genera in Table 1 is an accurate representation of intrafamilial relationships as I presently understand them.) Accession numbers are provided for each sample; numbers preceded by "P-" are those of James W. Walker, while those preceded by "PS-" are those of the author. These are also the same as the numbers on the permanent light slides. Accession numbers for samples illustrated in the present work appear in **boldface** in the following accounts.

RESULTS: SUMMARY OF DATA

Composite Description of External Pollen Morphology in the Family Araceae

Species Examined: 380/2,500; genera 99/105; subgenera and sections 98/114.

POLLEN TYPE: *aperture type* monosulcate (*Gymnostachys*, Potheae, Lasieae, Symplocarpeae) to monosulcoidate (*Stylochaeton* sect. *Spirogyne*), extended monosulcate or zonate (Zamioculcadeae, Monstereae), diaperturate (*Calla*, *Heteropsis* spp., *Rhaphidophora peeploides*), forate (*Anthurium*), or inaperturate (remaining taxa); *polarity* heteropolar (monosulcate grains) to isopolar (zonate, diaperturate, and many inaperturate grains) to apolar (forate and many inaperturate grains). POLLEN SHAPE boat-shaped-elongate (*Orontium*, some *Philodendron* spp., *Spathicarpa*, and others) to boat-shaped-elliptic (most monosulcate and diaperturate grains; many inaperturate grains) to "hamburger-shaped" (zonate grains) to globose (forate and many inaperturate grains); *symmetry* bilateral (monosulcate grains) to monosymmetric (most zonate grains) or isobisymmetric (some zonate and diaperturate grains) to radiosymmetric (forate and many globose, inaperturate grains). POLLEN-UNIT monads; tetrads only in *Xanthosoma* and *Chlorospatha*. POLLEN SIZE medium-sized; mean 37 μm, range 12 (*Homalomena* cf. *versteegii*)–106 (*Pseudohydrosme gabunense*) μm. EXINE SCULPTURING: *nonapertural exine* microreticulate or foveolate to reticulate, spinulose-reticulate, striate-reticulate, retiverrucate; spinulose-pilate to papillate, verrucate, or, rarely, gemmate, rugulate, or tuberculate; striate to plicate, striate-verrucate; spinose or psilate, fossulate, scabrate, etc.; *apertural exine* psilate to coarsely verrucate (e.g., in *Symplocarpus foetidus*), very rarely spinulose (*Anthurium margaricarpum*). EXINE STRUCTURE: *nonapertural exine* columellate in *Zamioculcas* and *Anthurium*, granular in *Cyrtosperma* and perhaps *Arisaema*; unknown or ambiguous otherwise; *apertural exine* unknown. EXINE STRATIFICATION with endexine in *Zamioculcas*, *Anthurium*, *Spathiphyllum*, and *Cyrtosperma*; endexine perhaps absent from *Arisaema*; unknown for remaining genera.

Index to Aroid Pollen Descriptions and Figures

Genus[a]	Description, p.:	Figures[b]
Acorus L. [Acoraceae]	9	1–3; 398, 436
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Aglaonema Schott	19	170–173
Alloschemone Schott	15	107, 108
Alocasia (Schott) Don	31	320–325; 427
Ambrosina Bassi	38	394, 395; 466
Amorphophallus Blume ex Decne.	36	364–387; 434, 447, 463
Amydrium Schott	14	95–100
Anadendrum Schott	10	22, 23; 415, 472
Anaphyllopsis A. Hay	17	141, 142; 443
Anaphyllum Schott	18	145, 146
Anchomanes Schott	28	264–267
Anthurium Schott	11	24–62; 413, 450, 457–459, 473, 480
Anubias Schott	20	176, 177
Aphyllarum S. Moore (syn. **Caladium**)		
Aridarum Ridley	21	186, 187
Ariopsis Nimmo	35	357, 358
Arisaema C. Martius	34	354–356; 488
Arisarum Hill	38	392, 393; 465
Arophyton Jum.	25	237, 238
Arum L.	32	333–335
Asterostigma Fischer & C. Meyer	25	239–243; 418
Biarum Schott	34	348, 349, 352, 353
Bognera Mayo & Nicolson	23	220, 221
Bucephalandra Schott	21	[not illustrated]
Caladiopsis Engl. (syn. **Chlorospatha**)		
Caladium Vent.	29	279–281
Calla L.	17	133–136; 412
Callopsis Engl.	28	272–274; 483
Carlephyton Jum.	25	233, 234
Cercestis Schott	27	258–261
Chlorospatha Engl.	30	286–289; 455, 479
Colletogyne Buchet	25	235, 236; 422
Colocasia Schott	31	308–313; 462, 484
Cryptocoryne	23	222–224
Culcasia P. Beauv.	10	20, 21; 414, 468
Cyrtosperma Griffith	17	137, 138
Diandriella Engl. (syn. **Homalomena**)		
Dieffenbachia Schott	23	210–219; 423, 444
Dracontioides Engl.	18	151, 152
Dracontium L.	18	153–159; 402
Dracunculus Hill	33	336, 337
Echidnium Schott (syn. **Dracontium**)		
Eminium (Blume) Schott	34	347, 351
Epipremnum Schott	15	101–104; 408, 409
Filarum Nicolson	24	227, 228
Furtadoa M. Hotta	19	162, 163; 478
Gearum N. E. Br.	26	[not illustrated]
Gonatanthus Klotzsch	31	314, 315; 485
Gonatopus Hook. f.	10	15–17, 19; 405, 449
Gorgonidium Schott	26	250–253; 469
Gymnostachys R. Br.	9	4, 5; 399, 437
Hapaline Schott	31	318, 319
Helicodiceros Schott	33	[not illustrated]

INDEX TO AROID POLLEN DESCRIPTIONS AND FIGURES, CONTINUED

INDEX TO AROID POLLEN DESCRIPTIONS AND FIGURES, CONTINUED

Genus[a]	Description, p.:	Figures[b]
Ulearum Engl.	24	229, 230
Urospatha Schott	18	149, 150
Urospathella Bunting (syn. **Urospatha**)		
Xanthosoma Schott	29	282–285; 429, 445
Xenophya Schott (syn. **Alocasia**)		
Zamioculcas Schott	10	13, 14, 18; 404
Zantedeschia Sprengel	20	174, 175
Zomicarpa Schott	24	231, 232; 482
Zomicarpella N. E. Br.	24	[not illustrated]

[a] The disposition of generic names relegated to synonymy since 1978 is indicated; previously synonymized names were similarly dealt with by Bogner (1978).

[b] The number(s) to the right of the semicolon (where present) refer to figures in the various summary plates; except in the case of *Calla*, these are always duplicates of figures from the taxonomically organized section (figures to the left of the semicolon). Where no semicolon is present, all numbers refer to figures in the taxonomic grouping.

Formal Descriptions of External Pollen Morphology at the Generic Level

Genus: **Acorus** L. [Acoraceae] Figures 1–3; 398, 436.

Taxonomic Reference: Engler, 1905.

Published SEM Micrographs: A. calamus (Dahlgren & Clifford, 1982).

Published TEM Micrographs: A. calamus (Tarasevich, 1989).

Species Examined: 2/2.

POLLEN TYPE: *aperture type* monosulcate to subulcerate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 18 µm, range 15 (*A. gramineus*)–20 (*A. calamus*) µm. EXINE SCULPTURING: *nonapertural exine* shallowly and remotely (*A. calamus*) or more densely (*A. gramineus*) foveolate, otherwise psilate; *apertural exine* subpsilate. EXINE STRUCTURE tectate-columellate, according to the TEM micrograph published by Tarasevich (1989). EXINE STRATIFICATION endexine is not indicated in the TEM micrograph of Tarasevich (1989).

REMARKS: *Acorus* is no longer considered a member of the Araceae (Grayum, 1987, 1990; Bogner & Nicolson, 1991; Duvall et al., 1992), but was so treated a priori for the present study, and may be referred to as an "aroid" elsewhere in this paper. Asian authors (Zhu, 1985) distinguish as many as six species in this genus.

Specimens Examined: A. calamus L. (**PS-1**), *Zika 655* (MASS), Vermont. *A. gramineus* Sol. (**PS-2**), *Kurosaki 7178* (MASS), Japan.

Genus: **Gymnostachys** R. Br. Figures 4, 5; 399, 437.

Taxonomic Reference: Engler, 1905.

Published SEM Micrographs: G. anceps (Bogner, 1987).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 31 µm, range 30–33 µm. EXINE SCULPTURING: *nonapertural exine* foveolate to slightly fossulate; *apertural exine* fossulate-verrucate.

Specimens Examined: G. anceps R. Br. (PS-495), cult. Petersham, Mass.; (**P-3293**), *Constable 30942* (K), Australia; (P-3541), *Nicolson 1382* (US), Australia.

Genus: **Pothos** L. Figures 6–10; 400, 438.

Taxonomic Reference: Engler, 1905.

Published SEM Micrographs: P. scandens (Straka & Friedrich, 1984).

Species Examined: 7/50; *sections* 2/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 21 µm, range 16 (*P. remotiflorus*)–25 (*P. repens*) µm. Pollen of sect. *Pothos* (mean 24 µm, range 21–25 µm) is consistently larger than that of sect. *Allopothos* (mean 18 µm, range 16–21 µm). EXINE SCULPTURING: *nonapertural exine* foveolate to reticulate or subrugulate; muri psilate or minutely tuberculate (sect. *Allopothos*); *apertural exine* foveolate to rugulate or verrucate, generally similar to the nonapertural exine.

REMARKS: Pollen of the two sections is distinguishable by size and exine characters, as noted above.

Specimens Examined: P. albertisii Engl.-P (P-3578), *Leach NGF 34273* (US), New Guinea. *P. beccarianus* Schott-A, *Martin & Ismawi S36660* (L [PS-201]; MO [**PS-433**]), Sarawak. *P. hookeri* Schott-P (P-3535), *Nicolson 4252* (US), Ceylon [Sri Lanka]; *Bremer & Bremer 935* (US), Ceylon [Sri Lanka]. *P. latifolius* Hook. f.-A (P-3295), *Put 3615* (K), Siam [Thailand]. *P. remotiflorus* Hook.-A (**P-3576**), *Jayasuriya & Dassanayake 1016* (US), Ceylon [Sri Lanka]. *P. repens* (Lour.) Merr.-P (**P-3296**), *Morse 501* (K), China. *P. rumphii* (C. Presl) Schott-A (P-3579), *Lavarack & Ridsdale NGF 31188* (US), New Guinea. *P. scandens* L.-P (**P-3294**), *Charoenphol et al. 3566* (K), Thailand; *Sivadasan CU 13128* (US), India. *Section Annotations:* A = *Allopothos* Schott; P = *Pothos.*

Genus: **Pedicellarum** M. Hotta [Not illustrated.]

Taxonomic Reference: Hotta, 1976.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean *18 µm. EXINE SCULPTURING: *nonapertural exine* reticulate, the muri minutely tuberculate; *apertural exine* not seen.

REMARKS: Pollen of this genus is identical in all respects to that of species in *Pothos* sect. *Allopothos* (e.g., *P. remotiflorus, P. latifolius*). Sample PS-433, previously (Grayum, 1984) believed to represent *Pedicellarum,* is now known to have been taken from a misidentified specimen of *Pothos beccarianus* (P. Boyce, in litt.). This disclosure has a significant bearing on statements relating to *Pedicellarum* in Grayum (1990; see especially p. 670).

Specimens Examined: P. paiei M. Hotta, *bin Paie S16354* (SAR [PS-168]; L [PS-200]), Sarawak.

Genus: **Pothoidium** Schott Figures 11, 12; 448.

Taxonomic Reference: Engler, 1905.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 26 μm. EXINE SCULPTURING: *nonapertural exine* reticulate with psilate muri; *apertural exine* shallowly fossulate or verrucate.

REMARKS: Pollen of this genus is similar in all respects to that of *Pothos* sect. *Pothos*.

Specimen Examined: P. lobbianum Schott (**P-3536**), *Borden Forestry Bureau No. 3053* (US), Philippines.

Genus: **Zamioculcas** Schott Figures 13, 14, 18; 404.

Taxonomic Reference: Engler, 1905.

Published TEM Micrographs: Z. zamiifolia (Tarasevich, 1989).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* extended monosulcate to perhaps fully zonate; grains surviving acetolysis intact; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 60 μm. EXINE SCULPTURING: *nonapertural exine* fossulate-foveolate; *apertural exine* verrucate. EXINE STRUCTURE tectate-columellate (Tarasevich, 1989). EXINE STRATIFICATION endexine is depicted in the TEM micrograph published by Tarasevich (1989).

REMARKS: The exine in this genus is up to 3.5 μm thick.

Specimen Examined: Z. zamiifolia (Lodd.) Engl. (**PS-151**), *Peter s.n.* (M), Tanzania (cult. M).

Genus: **Gonatopus** Hook. f. Figures 15–17, 19; 405, 449.

Taxonomic Reference: Engler, 1905.

Published SEM Micrographs: G. boivinii (Bogner, 1987); *G. rhizomatosus* (Obermeyer, 1977).

Species Examined: 2/5.

POLLEN TYPE: *aperture type* extended monosulcate or fully zonate, even in the same sample; the grains survive acetolysis intact; *polarity* heteropolar or subisopolar. POLLEN SHAPE boat-shaped-elliptic to hamburger-shaped; *symmetry* bilateral or monosymmetric. POLLEN-UNIT monads. POLLEN SIZE large; mean 76 μm, range 73–79 μm. EXINE SCULPTURING: *nonapertural exine* foveolate, the foveolae scattered (*G. boivinii*) or aggregated in fossulae (*G. angustus*); *apertural exine* psilate to verrucate.

REMARKS: The pollen illustrated in Obermeyer (1977) is unexpanded. According to J. Bogner (in litt.), *G. rhizomatosus* is a synonym of *G. angustus*. The exine in this genus is quite thick—up to 6.5 μm in *G. angustus*.

Specimens Examined: G. angustus N. E. Br. (**PS-274**), *Bogner 1664* (M), cult. M (orig. South Africa). *G. boivinii* (Decne.) Engl. (PS-521), cult. K (acc. no. 494-67.49402).

Genus: **Culcasia** P. Beauv. Figures 20, 21; 414, 468.

Taxonomic Reference: Engler, 1905.

Published SEM Micrographs: C. rotundifolia (Bogner, 1980a); *C. angolensis, C. liberica, C. longevaginata, C. scandens, C. tepoensis* (Knecht, 1983a, b); *C. parviflora, C. piperoides* (detail only), *C. saxatilis, C. tenuifolia* (Knecht, 1983a).

Species Examined: 3/20.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 27 (*C. rotundifolia*)–40 (*C. longevaginata*) μm. EXINE SCULPTURING verrucate to rugulate or subreticulate, usually with psilate patches that may be small and scattered or occupy at least half the grain (e.g., in some grains of *C. lancifolia*).

REMARKS: The pollen is reminiscent of that of *Nephthytis* sect. *Oligogynium*, *Gorgonidium mirabile*, etc. Pollen of *Culcasia* has been studied extensively at the SEM level by Knecht (1983a, b). Most species examined by her have verrucate pollen more or less similar to that illustrated in this paper, varying somewhat in the size of the verrucae and their density on the surface of the grain. Pollen of *C. tepoensis* and *C. liberica* has rather large verrucae, and in the latter species the verrucae are composed of minute "granular protuberances" (as are the muri in pollen of *Rhaphidophora africana*). Pollen of *C. angolensis* is unique in being spinose.

Specimens Examined: C. lancifolia N. E. Br. (PS-186), *Louis 107* (NY), Belgian Congo [Zaire]. *C. longevaginata* Engl. (**PS-238**), *Knecht s.n.* (M), Ivory Coast (cult. M). *C. rotundifolia* Bogner (PS-170), *Bogner 749* (M), Gabon.

Genus: **Anadendrum** Schott Figures 22, 23; 415, 472.

Taxonomic Reference: Engler, 1905.

Species Examined: 3/9.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 µm (*A. montanum*). EXINE SCULPTURING pilate or subretipilate, the pilae spinulose-tipped and solitary, or united in groups of 2–4 or more.

Specimens Examined: A. marginatum (Wallich) Schott (P-3580), *Nicolson 1065* (US), Malaya. *A. microstachyum* (Vriese & Miq.) Backer & Alderw. (P-3537), *Hardial 117* (US), Singapore. *A. montanum* Schott (**PS-176**), *Clemens & Clemens 3818* (NY), Annam [Vietnam].

Genus: **Anthurium** Schott Figures 24–62; 413, 450, 457–459, 473, 480.

Taxonomic References: Engler, 1905; Croat, 1983, 1985; Croat & Sheffer, 1983.

Published SEM Micrographs: A. armeniense, A. colonicum (Croat, 1980); *A. bakeri, A. leuconeurum, A. martianum, A. elegans* (detail only), *A. podophyllum* (detail only), *A. gracile* (detail only), *A. pedatoradiatum* (detail only), *A. hybridum, A. digitatum, A. scandens, A. willdenowii* (detail only), *A. crystallinum* (Tarasevich, 1989).

Published TEM Micrographs: Anthurium sp. indet. (Gullvåg, 1966; Chanda & Rowley, 1967; Rowley & Southworth, 1967); *A. magnificum, A. pedatoradiatum, A. scherzerianum, A. podophyllum, A. digitatum* (Tarasevich, 1989).

Species Examined: 53/1,000; *sections* 19/19.

POLLEN TYPE: *aperture type* diporate to more frequently forate; very rarely inaperturate (sect. *Polyphyllium*). The number and arrangement of apertures on these small grains is often difficult to determine; 3–4 pores is the most common condition, the maximum number visible from any aspect in SEM photos being 4 (in *A. bellum*); *polarity* apolar. POLLEN SHAPE spherical to subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 µm, range 14 (*A. pallidiflorum*)–29 (*A. magnificum*) µm. The smallest pollen occurs in sects. *Porphyrochitonium* (mean 17 µm) and *Anthurium* (mean 17 µm, range 14 24 µm), the largest in sect. *Cardiolonchium* (mean 25 µm) and the monotypic sect. *Leptanthurium* (mean 24 µm). EXINE SCULPTURING: *nonapertural exine* basically foveolate to reticulate or subrugulate (*A. bellum, A. ovatifolium, A. polyschistum, A. redolens, A. salvadorense*), the muri psilate or nearly so (*A. andraeanum, A. comtum, A. consobrinum, A. crenatum, A. dominicense, A. erskinei, A. gymnopus, A. leucostachyum, A. magnificum, A. ovandense, A. oxycarpum, A. pentaphyllum, A. pittieri, A. pulchellum, A. radicans, A. veitchii*), or studded with minute, square-tipped spinules (*A. bellum, A. crassinervium, A. curvispadix, A. deflexum, A. gracile, A. luteynii, A. margaricarpum, A. nervatum, A. pedatum, A. protensum, A. purpureospathum, A. reticulatum, A. scandens, A. standleyi, A. validifolium, A. willdenowii*). A rather distinctive series comprises pollen with peculiarly "criss-crossing" or overlapping, psilate (*A. fragrantissimum, A. lucens*) or spinulose muri forming a very tight (*A. lancea, A. nitidum, A. rivulare, A. subcoerulescens*) or more open (*A. harrisii* and especially *A. chiapasense, A. longipeltatum, A. scherzerianum*) reticulum. Low, broad, smoothly contoured muri are fairly uncommon (*A. magnificum, A. ovandense, A. radicans, A. tilaranense*), and spinulose muri of the same description even more so (*A. amazonicum*). *Anthurium pallidiflorum* and *A. amazonicum* are unusual in that large portions of the surface area of the grains are without reticulum or foveolae. The extremes in reticulum size are infrequent; the definitively foveolate grains of *A. pallidiflorum* are unique in the material examined, as are the openly reticulate grains of *A. redolens*. In section *Polyphyllium* (*A. clidemioides, A. flexile*) and in *A. friedrichsthalii*, a reticulum is obsolete or lacking altogether. The last-mentioned species is further unique in having truly spinose grains, and sect. *Polyphyllium* in having gemmate pollen (with the gemmae obscurely rugose); *apertural exine* mostly psilate, rarely spinulose (*A. margaricarpum*). EXINE STRUCTURE tectate-columellate (Tarasevich, 1989). EXINE STRATIFICATION Chanda & Rowley (1967) described a "nexine 2," which is presumably equivalent to endexine; Tarasevich (1989) depicts endexine in several species of *Anthurium*.

REMARKS: Little can be said about size and sculpturing variations at the sectional level, since usually only one or two members of a section were examined. Sections *Polyphyllium, Oxycarpium, Polyneurium*, and *Pachyneurium* are quite uniform; 10 species of the latter were studied, and only *A. salvadorense* is distinctive. Sections *Xialophyllium, Porphyrochitonium, Belolonchium*, and *Anthurium*, on the other hand, display considerable diversity.

Section *Polyphyllium*, with inaperturate, gemmate pollen lacking any trace of a reticulum, stands sharply apart from the rest of the genus.

Tarasevich (1989) classified exine sculpturing in *Anthurium* into four types and seven subtypes, but there seems little point in arbitrarily partitioning what is clearly a continuum of variation.

I have followed the conclusions of Mayo (1981) in accepting sect. *Urospadix* Engl. as the autonymic section in *Anthurium*.

Specimens Examined: A. amazonicum Engl.?-Ca (**P-3767**), *Mattos & Mattos 10177* (US), Brazil. *A. andraeanum* Linden-Cm (PS-146), *Torrey s.n.* (MASS), cult. Massachusetts. *A. bellum* Schott-A (**PS-153**), *Harley 17571* (K), Brazil, cult. K (acc. no. 131-74.01527). *A. chiapasense* Standley subsp. *tlaxiacense* (Matuda) Croat-B (PS-213), *Croat 45927* (MO), Mexico. *A. clidemioides* Standley-Pp (**PS-109**), *Grayum 1945* (DUKE), Costa Rica. *A. comtum* Schott-A (P-3762), *Engler 220* (US), cult. KIEL (orig. Brazil). *A. consobrinum* Schott-Pa (**P-3766**), *Taylor 18163* (US), Costa Rica. *A. crassinervium* (Jacq.) Schott-Pa (P-3753), *Engler 249* (US), cult. B. *A. crenatum* (L.) Kunth-Pa (PS-147), *Heller 6283* (MASS), Puerto Rico. *A. curvispadix* Croat-Cm (PS-214), *Croat 44730* (MO), Panama. *A. deflexum* Engl.-A (P-3763), *Killip & Smith 17065* (US), Colombia. *A. dominicense* Schott-E (**PS-5**), *Hodge 1771* (MASS), Dominica. *A. erskinei* Mayo-A (PS-154), *Erskine 34* (K), Brazil, cult. K (acc. no. 059-74.00786). *A. flexile* Schott-Pp (P-3754), *Johnson 1257* (US), Guatemala. *A. fragrantissimum* Croat-Pc (PS-229), *Folsom 3184* (MO). *A. friedrichsthalii* Schott-Pc (**P-3755**), *Liesner 1930* (US), Costa Rica. *A. gracile* Engl.-L (**PS-155**), *Leppard 1406* (K), Colombia, cult. K (acc. no. 019-75.00108). *A. gymnopus* Griseb.-G (**P-3764**), *Wright 3210* (US), Cuba. *A. harrisii* (Graham) Endl.-A (**PS-215**), *Croat 38340* (MO) cult. Venezuela. *A. lancea* Sodiro-B (**P-3769**), *Dodson 5767* (US), Ecuador. *A. leucostachyum* Sodiro-Cm (**P-3768**), *Croat 38691* (US), Ecuador. *A. llanense* Croat subsp. *oblongispicum* Croat & Grayum subsp. ined.-A (PS-523), *Grayum 3186* (DUKE), Costa Rica. *A. longipeltatum* Matuda-B (**PS-216**), *Croat 43906* (MO), Mexico. *A. lucens* Standley ex Yuncker-B (**PS-217**), *Croat 46656* (MO). *A. luteynii* Croat-Pa (PS-218), *Croat 25521* (MO), Panama. *A. magnificum* Linden-Ca (**PS-276**), *Grayum 3268* (MASS), cult. MASS. *A. margaricarpum* Sodiro-T (P-3751), *Oldeman et al. 36* (US), Ecuador. *A. nervatum* Croat-Pa (PS-219), *Croat 37443* (MO), Panama. *A. nitidum* Benth.-B (P-3770), *Killip & Smith 18845* (US), Colombia. *A. ovandense* Matuda-B (**PS-220**), *Croat 46164* (MO), Mexico. *A. ovatifolium* Sodiro-Dn (**P-3773**), *Kirkbride & Chamba R. 4098* (US), Ecuador. *A. oxycarpum* Poeppig-O (P-3757), *E. Forero et al. 6315* (US), Brazil. *A. pallidiflorum* Engl.-A (**PS-156**), cult. K (acc. no. 132-78.01271; orig. Ecuador). *A. pedatum* (Kunth) Kunth-Sz (**P-3772**), *Grant & Drew 10662* (US), Colombia. *A. pentaphyllum* (Aublet) Don var. *bombacifolium* (Schott) Madison-Dp (PS-110), *Grayum 1948* (DUKE), Costa Rica. *A. pittieri* Engl.-O (**P-3756**), *Standley & Torres R. 51774*, Costa Rica. *A. polyschistum* R. Schultes & Idrobo-Dp (**P-3582**), *Meyer & Mazzeo 10881* (US), cult. Georgia. *A. protensum* Schott-Pa (**P-3765**), *Standley 36334* (US), Costa Rica. *A. pulchellum* Engl.-X (P-3758), *Cuatrecasas 22222* (US), Colombia. *A. purpureospathum* Croat-Pa (PS-223), *Croat 38094* (MO), Panama. *A. radicans* K. Koch-Ch (**PS-206**), *Madison 3725* (MO), cult. SEL (orig. Brazil). *A. redolens* Croat-Pc (**PS-224**), cult. MO (orig. Panama). *A. reticulatum* Benth.-Pn (**P-3760**), *Kyburz 7* (US), Colombia. *A. rivulare* Sodiro-X (**P-3759**), *Madison & Besse 7178* (US), Ecuador. *A. salvadorense* Croat-Pa (**PS-225**), *Croat 42092* (MO), El Salvador. *A. scandens* (Aublet) Engl. var. *leucocarpum* (Schott) Engl.-T (**PS-148**), *Broadway s.n.* (MASS), Trinidad. *A. scherzerianum* Schott-Pc (**P-3752**), *Lellinger 1486* (US), Costa Rica. *A. standleyi* Croat & R. A. Baker-Pa (PS-226), *Croat 43439* (MO), Costa Rica. *A. subcoerulescens* Engl.-Pn (**P-3761**), *Dodson 5718* (US), Ecuador. *A. tilaranense* Standley-Sm (**P-3771**), *Standley & Valerio 45586* (US), Costa Rica. *A. trinerve* Miq.-T (PS-441), *Ahles s.n.* (MASS). *A. validifolium* K. Krause-Pa (**PS-227**), *Croat 10667* (MO). *A. veitchii* Masters-Cm (PS-228), *Fennell 2* (MO), Colombia. *A. willdenowii* Kunth-A (**PS-158**), *Bannochie s.n.* (K), Barbados, cult. K (acc. no. 382-68.38216). SECTION ANNOTATIONS: A = *Anthurium*; B = *Belolonchium* Schott; Ca = *Cardiolonchium* Schott; Ch = *Chamaerepium* Schott; Cm = *Calomystrium* Schott; Dn = *Digitinervium* Sodiro; Dp = *Dactylophyllium* Schott; E = *Episeiostenium* Schott; G = *Gymnopodium* Engl.; L = *Leptanthurium* Schott; O = *Oxycarpium* Schott; Pc = *Porphyrochitonium* Schott; Pa = *Pachyneurium* Schott; Pn = *Polyneurium* Engl.; Pp = *Polyphyllium* Engl.; Sm = *Semaeophyllium* Schott; Sz = *Schizoplacium* Schott; T = *Tetraspermium* Schott; X = *Xialophyllium* Schott.

Genus: **Spathiphyllum** Schott Figures 63–68; 416, 460.

Taxonomic References: Bunting, 1960b; Nicolson, 1968b.

Published SEM Micrographs: S. blandum (Lugardon et al., 1988); *S. schomburgkii* (Grayum, 1986c).

Published TEM Micrographs: S. brevirostre (Lugardon et al., 1988); *S. wallisii* (Trevisan, 1980).

Species Examined: 15/63; *sections* 4/4.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-oblong to -elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 27 (*S. atrovirens*)–41 (*S. floribundum*) μm; of the two large sections, pollen of sect. *Spathiphyllum* (mean 30 μm, range 27–31 μm) is consistently smaller than that of sect. *Amomophyllum* (mean 35 μm, range 32–41 μm). Mean pollen size of sect. *Massowia* is 32 μm; that of the monotypic sect. *Dysspathiphyllum* is 34 μm. EXINE SCULPTURING striate, the psilate striae varying in thickness depending on the species but usually somewhat broader than the intervening furrows. Striae ± parallel, usually anastomosing to a greater or lesser extent, converging at each end of the grain into a psilate subcircular end plate. Columellae usually evident at base of striae. EXINE STRUCTURE according to Trevisan (1980) with each ridge or striation composing a tectate structure supported internally by columellae of variable size that are thickest toward the base. Lugardon et al. (1988) described a similar structure for exine of *Spathiphyllum* and *Holochlamys*, but with a granular infratectum. EXINE STRATIFICATION described by Trevisan (1980) as an "endexinous foot layer" underlying each ridge and forming the floor of each "valley"; Lugardon et al. (1988) confirmed the presence of endexine in *Spathiphyllum*.

REMARKS: This is perhaps the only aroid genus for which the disposition of the pollen in the tetrad stage has been studied (excepting genera with permanent tetrads). Huynh (1975) found that the "ends" of the grain (of *S. wallisii*), toward which the striae converge, are actually lateral faces; the long axis of the grain represents an equatorial axis, the polar axis being one of the infinite number of subequal small axes, and thus impossible to identify. He considered the pollen to be isopolar rather than heteropolar. The pollen of *Spathiphyllum* (and specifically *S. wallisii*) must rank as the best known in the family, considering the pollen-tetrad and TEM work cited above. Huynh's analysis of polarity is exactly what one would expect if the boat-shaped or elliptic appearance of these grains were due to recent derivation from a monosulcate predecessor.

Specimens Examined: S. atrovirens Schott-S (PS-362), *Hammel 12827* (DUKE), Costa Rica. *S. cannifolium*

(Dryander ex Sims) Schott-M (P-3610), *Peterson J-1490* (US), cult. KEN (acc. no. 701263). *S. cochlearispathum* (Liebm.) Engl.-S (P-3459), *Meagher 951* (TEX), cult. Miami (orig. Mexico). *S. floribundum* (Linden & André) N. E. Br.-A (PS-172), *Bogner 1665* (M), cult. M. *S. friedrichsthalii* Schott-S (P-3547), *Kruse Herb. 823* (US), Mexico. *S. fulvovirens* Schott-A (P-3611), *Kennedy & Foster 2160* (US), Panama. *S. gardneri* Schott-A (P-3614), *Eiten & Eiten 9040* (US), Brazil. *S. humboldtii* Schott?-D (P-3615), *Macedo 4036* (US), Brazil. *S. kalbreyeri* Bunting-A (**P-3612**), *Standley 29846* (US), Panama. *S. kochii* Engl.-S (P-3609), *Meyer & Mazzeo 10856* (US), cult. Georgia. *S. laeve* Engl.-M (**PS-114**), *Sperry 717* (DUKE), Costa Rica. *S. phryniifolium* Schott-S (P-3613), *Erlanson 353* (US), Panama. *S. schomburgkii* Schott-A (**P-3616**), *Dressler 3007* (US), Venezuela. *S. wendlandii* Schott-S (PS-514), *Hammel 8611* (DUKE), Costa Rica. *S.* sp. indet.-M (PS-319), *Hartley 12699* (A/GH), New Guinea. *Section Annotations:* A = *Amomophyllum* (Engl.) Engl.; D = *Dysspathiphyllum* Engl.; M = *Massowia* (K. Koch) Engl.; S = *Spathiphyllum.*

Genus: **Holochlamys** Engl. Figures 69–72.

Taxonomic Reference: Engler & Krause, 1908.

Published SEM Micrographs: H. beccarii (Lugardon et al., 1988; including cross section).

Species Examined: 2/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* heteropolar (due to the pattern of striae described below). POLLEN SHAPE boat-shaped-elliptic; *symmetry* asymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm, range 32–34 μm. EXINE SCULPTURING similar in all respects to that of *Spathiphyllum*, except for the fundamentally different and conceptually intricate pattern of the striae (see "Remarks"). EXINE STRUCTURE described by Lugardon et al. (1988) (see under *Spathiphyllum*). EXINE STRATIFICATION predicted by Lugardon et al. (1988) to feature an endexine, as in *Spathiphyllum*; however, they did not study pollen of *Holochlamys* using TEM.

REMARKS: For the sake of explanation, the *Holochlamys* pollen grain is best visualized as a sort of rectangular solid—i.e., with six faces, four "laterals" and two "ends." All of the striae converge at one of the ends. Only about half of the striae, however, also converge at the other (opposite) end; these doubly convergent striae occupy opposing faces (they are skewed somewhat from perfect opposition) of the grain. When viewed from either of these faces, a *Holochlamys* pollen grain appears identical to a grain of *Spathiphyllum*. Striae on the remaining two opposing lateral faces do not converge at the other end, but remain parallel, forming a band that nearly encircles the entire grain. Viewed from either of these lateral faces, all striae appear parallel (since the perspective is unfavorable for detecting the convergence on the adjacent *Spathiphyllum*-like faces, though some of the striae can be seen). Viewed from the second (nonconverging) end face, a pattern reminiscent of that formed by the two pieces of rawhide on a baseball is observable. Thus the *Holochlamys* pattern of striation (occurring also in *Steudnera* and *Protarum*) is hereby dubbed the "baseball" pattern, as opposed to the "football" pattern of *Spathiphyllum*, in which all striae converge at both ends of an isopolar grain.

Specimens Examined: H. beccarii (Engl.) Engl. (PS-515), *Bogner 1269* (M), cult. M. *H. guineensis* Engl. & K. Krause (**P-3548**), *Peterson 1449* (US), cult. KEN (acc. no. 701264); (P-3617), *Peterson J-1090* (US), cult. KEN (acc. no. 68849).

Genus: **Heteropsis** Kunth Figures 73–76; 410, 439.

Taxonomic Reference: Engler, 1905.

Species Examined: 4/13.

POLLEN TYPE: *aperture type* zonate (*H. oblongifolia, H. macrophylla, H. jenmanii*) or dicolpate (*H. integerrima*). The zonate grains of *H. oblongifolia* remain intact following acetolysis; however, no evidence of a "hinge" could be seen at the SEM level; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong or hamburger-shaped; *symmetry* bilateral or monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm, range 37 (*H. oblongifolia*)–42 (*H. integerrima*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate or foveolate-fossulate; *apertural exine* psilate.

REMARKS: Thanikaimoni (1969) described pollen of *H. spruceana* as dicolpate and that of *H. peruviana* as zonate; according to Erdtman (1952), pollen of *H. salicifolia* is zonate.

Specimens Examined: H. integerrima (Vell. Conc.) Stellf. (**PS-192**), *Prance et al. P25577* (NY), Brazil. *H. jenmanii* Oliver (PS-193), *Bernardi 2762* (NY), Venezuela. *H. macrophylla* A. C. Smith (P-3538), *Steward & Ramos P17656* (US), Brazil. *H. oblongifolia* Kunth (PS-339), *Gentry & Mori 13406* (A/GH), Panama; (**PS-359**), *Hammel 13079* (DUKE), Costa Rica; (P-3581), *Allen 5476* (US), Costa Rica.

Genus: **Rhaphidophora** Hassk. Figures 77–86; 411, 470.

Taxonomic Reference: Engler & Krause, 1908.

Species Examined: 8/60.

POLLEN TYPE: *aperture type* dicolpate (*R. peeploides*) or extended monosulcate (*R. reineckei, R. graeffei*) to perhaps fully zonate. Pollen of *R. africana* and *R. monticola* and some (but not all) grains of *R. reineckei* separates into halves upon acetolysis; *polarity* heteropolar or subisopolar. POLLEN SHAPE boat-shaped-elliptic or hamburger-shaped; *symmetry* bilateral or monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm, range 24 (*R. reineckei*) 55 (*R. monticola*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate (*R. montana*) or subreticulate (*R. peeploides*) to rugulate (*R. korthalsii*), fossulate (*R. graeffei*), scabrate (*R. pertusa*), retiscabrate (*R. africana*), verrucate (*R. reineckei*), or psilate (*R. monticola*); *apertural exine* psilate (*R. graeffei, R. peeploides*) or verrucate (*R. reineckei, R. monticola*); usually not observable.

REMARKS: This genus has on the average the smallest pollen in the tribe Monstereae, and the most diverse in terms of exine sculpturing. Although only eight species were examined, each is distinctive in this regard. Dicolpate pollen is reported from this genus for the first time here. Erdtman (1952) described the pollen of *R.* (= *Afrorhaphidophora*) *africana* as "(2–)3(–4)-sulculate (?)"; this was already rectified by Thanikaimoni (1969), although Dahlgren & Clifford (1982) did not incorporate the change. The material of this genus available for study in the present investigation was in general rather poor (with the exception of *R. peeploides* and *R. africana*), so it was not usually possible to distinguish between the extended monosulcate and fully zonate conditions (see "Remarks" under *Epipremnum*).

Specimens Examined: R. africana N. E. Br. (**PS-289**), *Bogner 708* (M), Gabon. *R. graeffei* Engl. (**P-3592**), *Whistler W743* (US), Samoa. *R. korthalsii* Schott (PS-342), *Bangham & Bangham 1008* (A/GH), Sumatra; (P-3593), *Anderson S31956* (US), Sarawak. *R. montana* (Blume) Schott (**P-3594**), *Nicolson 883* (US), cult. BO. *R. monticola* K. Krause (P-3596), *Ramos 23455* (US), Philippines. *R. peeploides* Engl. (**P-3544**), *Bunting 1619* (US), cult. BH. *R. pertusa* (Roxb.) Schott (**P-3591**), *Sivadasan CU19165* (US), India. *R. reineckei* Engl.? (**P-3595**), *Nicolson 1529* (US), Bougainville Is.

Genus: **Monstera** Adans. Figures 87–94; 406, 440, 451.

Taxonomic Reference: Madison, 1977.

Published SEM Micrographs: M. tenuis (Grayum, 1986c; detail only).

Species Examined: 10/60; *sections* 4/4.

POLLEN TYPE: *aperture type* fully zonate, separating into halves on acetolysis; *polarity* subisopolar. POLLEN SHAPE hamburger-shaped; *symmetry* monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 48 μm, range 40 (*M. diversifolia*)–52 (*M. tenuis*) μm. Pollen of the monotypic sections *Echinospadix* and *Tornelia* averages 49 μm and 50 μm, respectively; of the two large sections, sect. *Marcgraviopsis* has consistently larger pollen (mean 51 μm, range 49–52 μm) than sect. *Monstera* (mean 45 μm, range 40–49 μm). EXINE SCULPTURING: *nonapertural exine* densely foveolate (*M. acuminata, M. diversifolia, M. lechleriana, M. skutchii*) to subreticulate (*M. adansonii, M. oreophila, M. tenuis*), the brochi in *M. adansonii* reduced toward the aperture (at least on one half of the grain); sparsely and shallowly foveolate in *M. deliciosa*, completely psilate in *M. siltepecana, M. tuberculata; apertural exine* coarsely verrucate or rugulate in fresh material of *M. adansonii, M. dilacerata.*

REMARKS: The inner face of the exine in *M. deliciosa* is coarsely perforate. This was a chance observation that could not be evaluated for other species in the genus but might be considered in future studies. The genus is actually far more species-rich than indicated by Madison (1977).

Specimens Examined: M. acuminata K. Koch-Mg (P-3597), *Gutiérrez R. 75* (US), Mexico. *M. adansonii* Schott var. *laniata* (Schott) Madison-M (PS-383), *Hammel 13202* (DUKE), Costa Rica; (**P-3598**), *Chaves 204* (US), Nicaragua. *M. deliciosa* Liebm.-T (**PS-18**), *Torrey s.n.* (MASS), cult. MASS. *M. diversifolia* Croat & Grayum sp. ined.-M (**PS-386**), *Hammel 13159* (DUKE), Costa Rica; (P-3599), *Lent 824* (US), Costa Rica. *M. lechleriana* Schott-M (**P-3604**), *Dodson 5726* (US), Ecuador. *M. oreophila* Madison-M (PS-104), *Churchill 3697* (MASS), Costa Rica. *M. siltepecana* Matuda-M (P-3600), *J. D. Smith 1538* (US), Guatemala. *M. skutchii* Croat & Grayum sp. ined.-Mg (**P-3601**), *Skutch 5320* (US), Costa Rica. *M. tenuis* K. Koch-Mg (**P-3602**), *Lent 1589* (US), Costa Rica. *M. tuberculata* Lundell var. *brevinodum* (Standley & L. O. Williams) Madison-E (**PS-340**), *Madison 752* (A/GH), Costa Rica. *Section Annotations:* E = *Echinospadix* Madison; M = *Monstera*; Mg = *Marcgraviopsis* Madison; T = *Tornelia* (Gutiérrez ex Schott) Madison.

Genus: **Amydrium** Schott Figures 95–100.

Taxonomic Reference: Nicolson, 1968c.

Species Examined: 2/4.

POLLEN TYPE: *aperture type* fully zonate, the pollen separating into halves upon acetolysis; *polarity* subisopolar. POLLEN SHAPE hamburger-shaped; *symmetry* monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 39 μm, range 38 (*A. medium*)–41 (*A. humile*) μm. EXINE SCULPTURING: *nonapertural exine A. humile*—the type species of this originally monotypic genus—exhibits a rather peculiar type of exine sculpturing: the two unequal halves of the nonapertural exine are heteromorphic. The larger half is densely and minutely punctate, and the smaller half is virtually psilate (though obscurely verrucate and remotely punctate). *Amydrium medium*, included by Engler in the now-defunct genus *Epipremnopsis*, has uniformly foveolate-fossulate pollen; *apertural exine* psilate or obscurely verrucate.

Specimens Examined: A. humile Schott (**PS-177**), *Clemens & Clemens s.n.* (NY), cult. Singapore. *A. medium* (Zoll. & Moritzi) Nicolson (**P-3539**), *Hutchison 2762* (US), cult. Honolulu (orig. Philippines).

Genus: **Epipremnum** Schott Figures 101–104; 408, 409.

Taxonomic Reference: Engler & Krause, 1908.

Species Examined: 2/15.

POLLEN TYPE: *aperture type* fully zonate; most grains separating into two halves during acetolysis; *polarity* subisopolar. POLLEN SHAPE hamburger-shaped; *symmetry* monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm, range 36 (*E. pinnatum*)–44 (*E. dahlii*) μm. EXINE SCULPTURING: *nonapertural exine* in *E. pinnatum* somewhat similar to that in *Amydrium humile* though less extreme: one half of the nonapertural exine is foveolate-fossulate over the whole surface, the other half just centrally—the peripheral region being quite psilate to near the aperture. In *E. dahlii*, both halves are shallowly and remotely foveolate (i.e., virtually psilate); *apertural exine* coarsely verrucate in *E. pinnatum.*

REMARKS: Some authors (e.g., Hotta, 1970) prefer to submerge *Epipremnum* in *Rhaphidophora*. Although pollen of some species of the latter genus (e.g., *R. monticola*) might resemble that of *Epipremnum*, pollen of *Rhaphidophora* is in general smaller and more diversely sculptured than that of *Epipremnum*, and is less frequently fully zonate. Many more species need to be examined, however.

The distinctive pattern of exine sculpturing in *E. pinnatum* suggests that pollen morphology might be a way of deciding whether the widely cultivated *E. aureum* (Linden & André) Bunting (sometimes included in *Rhaphidophora* and formerly also in *Scindapsus* and even *Pothos*) is in reality a mere horticultural variety of that species, as Nicolson (1978) proposed. Polleniferous material of *E. aureum* could not be obtained for the present investigations.

Specimens Examined: E. dahlii Engl. (**P-3606**), *Streimann NGF 44156* (US), New Guinea. *E. pinnatum* (L.) Engl. (**P-3605**), *Nicolson 4260* (US), Ceylon [Sri Lanka].

Genus: **Scindapsus** Schott Figures 105, 106.

Taxonomic Reference: Engler & Krause, 1908.

Species Examined: 3/25.

POLLEN TYPE: *aperture type* fully zonate, separating into halves during acetolysis; *polarity* subisopolar. POLLEN SHAPE hamburger-shaped; *symmetry* isobisymmetric to monosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 38 μm, range 33 (*S. beccarii*)–45 (*S. splendidus*) μm. EXINE SCULPTURING: *nonapertural exine* shallowly and sparsely punctate, nearly psilate; *apertural exine* psilate or somewhat verrucate.

Specimens Examined: S. beccarii Engl. (PS-516), cult. MO, orig. cult. K (acc. no. 478-65.47801; orig. Sabah). *S. maclurei* (Merr.) Merr. & Metcalf (P-3608), *Nicolson 1620* (US), Thailand. *S. splendidus* Alderw. (**P-3546**), *Nicolson 853B* (US), cult. BO.

Genus: **Alloschemone** Schott Figures 107, 108.

Taxonomic Reference: Madison, 1976a.

Species Examined: 1/2.

POLLEN TYPE: *aperture type* disulcate?; *polarity* uncertain. POLLEN SHAPE uncertain; *symmetry* uncertain. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 46 μm. EXINE SCULPTURING: *nonapertural exine* shallowly foveolate; *apertural exine* not seen.

REMARKS: Madison (1976a) submerged this ditypic Amazonian genus into the otherwise wholly Asian *Scindapsus*, but later (Madison, 1979) expressed misgivings. Recent evidence (Carvell, 1989) supports the maintenance of *Alloschemone*. The fertile pollen material examined did not yield satisfactory, mature pollen grains; what little can be seen is intriguing if inconclusive, and additional fertile collections of this little-known species are needed.

Specimen Examined: A. occidentalis (Poeppig) Engl. & K. Krause (**PS-197**) [filed as *Scindapsus occidentalis* Poeppig], *Krukoff 7162* (NY), Brazil.

Genus: **Stenospermation** Schott Figures 109–118; 407, 417.

Taxonomic Reference: Engler & Krause, 1908; Gómez, 1983.

Published SEM Micrographs: S. multiovulatum, S. robustum (Gómez, 1983).

Species Examined: 8/60.

POLLEN TYPE: *aperture type* fully zonate and separating into halves during acetolysis (*S. angustifolium, S. popayanense, S. robustum, S. sessile, S. multiovulatum*) or inaperturate (*S.* sp. ined., *S.* sp. indet., probably also *S. marantifolium*). In *S. popayanense* and *S. multiovulatum*, the nonapertural halves of the exine are reduced to mere disklike caps dwarfed by the bulging aperture membrane in critical-point dried material. Pollen of *S. angustifolium* and *S. robustum* appears conventionally zonate; *polarity* subisopolar or apolar. POLLEN SHAPE hamburger-shaped or subspheroidal; *symmetry* isobisymmetric to monosymmetric or radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 42 μm, range 30 (*S.* sp. indet.)–58 (*S. popayanense*) μm. EXINE SCULPTURING: *nonapertural exine* psilate (*S. multiovulatum*) to shallowly and sparsely foveolate (*S. angustifolium, S. marantifolium, S. robustum, S. sessile*), fossulate-foveolate (*S. popayanense*), verrucate (*S.* sp. ined.), or baculate (*S.* sp. indet., with some large psilate patches); *apertural exine* virtually psilate.

REMARKS: There is no previous record of inaperturate pollen for this genus, nor for *Rhodospatha*. The present investigations have probably raised more questions than they have answered for these two genera; good polleniferous material for both is difficult to obtain.

Samples PS-242 and P-3542, though both identified as *S. popayanense*, are here treated as different species in view of their widely divergent pollen morphology.

Gómez (1983) pictured pollen of *S. multiovulatum* from the same collection as that illustrated here. Although appearing to be inaperturate, her grains are probably completely covered by pollenkitt.

Specimens Examined: S. angustifolium Hemsley (**PS-363**), *Hammel 12974* (DUKE), Costa Rica; (**P-3584**), *Ebinger 352* (US), Panama. *S. marantifolium* Hemsley (PS-167), cult. K (acc. no. 567-62.56708). *S. multiovulatum* (Engl.) N. E. Br. (**PS-207**), *Croat 33686* (MO), Panama. *S. popayanense* Schott (PS-242), *Bogner 463* (M), cult. M. *S. robustum* Engl. (P-3586), *Cook & Griggs 85* (US), Guatemala. *S. sessile* Engl. (P-3587), *Luteyn 3001* (US), Costa Rica. *S.* sp. indet. [filed as *S. popayanense* Schott] (**P-3542**), *Killip & García 33655* (US), Colombia. *S.* sp. ined. (**PS-122**), *Madison 3999* (SEL), Ecuador.

Genus: **Rhodospatha** Poeppig Figures 119–123; 441.

Taxonomic Reference: Engler & Krause, 1908.

Species Examined: 6/67.

POLLEN TYPE: *aperture type* fully zonate (*R. oblongata, R. roseospadix, R. venosa*) or inaperturate (*R. pellucida, R. wendlandii*, probably *R. moritziana*). Pollen of the zonate species separates into halves during acetolysis; *polarity* subisopolar to isopolar. POLLEN SHAPE hamburger-shaped or boat-shaped-elliptic to -oblong; *symmetry* monosymmetric or bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 47 μm, range 34 (*R. oblongata*)–57 (*R. moritziana*) μm. EXINE SCULPTURING: *nonapertural exine* densely (*R. roseospadix, R. moritziana*) to sparsely foveolate and nearly psilate (*R. oblongata*) to obscurely fossulate (*R. wendlandii, R. pellucida*) or verrucate (*R. venosa*); *apertural exine* coarsely verrucate in *R. oblongata*.

REMARKS: Inaperturate pollen has not been previously reported in this genus. See "Remarks" under *Stenospermation*.

Specimens Examined: R. moritziana Schott (PS-338), *Soejarto & Villa 2751* (A/GH), Colombia. *R. oblongata* Poeppig (**PS-416**), *Maguire & Fanshawe 22883* (K), Guyana. *R. pellucida* Croat & Grayum sp. ined. (**PS-370**), *Hammel 12726* (DUKE), Costa Rica. *R. roseospadix* (Matuda) Matuda (P-3589), *Matuda 18399* (US), Mexico. *R. venosa* Gleason (**P-3590**), *Irwin et al. 47857* (US), Brazil. *R. wendlandii* Schott ex Engl. (PS-337), *Plowman 3559* (A/GH), Colombia; (PS-369), *Hammel 13135* (DUKE), Costa Rica.

Genus: **Orontium** L. Figures 124, 125; 401, 442.

Taxonomic Reference: Krause, 1908.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elongate; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 64 μm, range 55–73 μm. EXINE SCULPTURING: *nonapertural exine* densely foveolate-fossulate; *apertural exine* not seen.

REMARKS: Note the rather striking difference in mean pollen size between two different collections of the same species.

Specimens Examined: O. aquaticum L. (PS-19), *Goodale 69938* (MASS), Alabama; (**PS-145**), *Ahles 10105* (MASS), Florida.

Genus: **Lysichiton** Schott Figures 126–130; 452.

Taxonomic Reference: Hultén & St. John, 1931.

Published SEM Micrographs: L. americanus (Grayum, 1986c).

Published TEM Micrographs: L. americanus (Hesse, 1980).

Species Examined: 2/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm, range 38 (*L. camtschatcensis*)–43 (*L. americanus*) μm. EXINE SCULPTURING: *nonapertural exine* reticulate (coarsely so in *L. americanus*), the brochi reduced toward the ± broadly marginate aperture; *apertural exine* not seen. EXINE STRUCTURE: *nonapertural exine* with low columellae partly fused to form a perforated tectum with comparatively well-developed infrasexinose chambers (Hesse, 1980).

REMARKS: Pollen morphology supports the recognition of two species of *Lysichiton*.

Specimens Examined: L. americanus Hultén & H. St. John (**PS-16**), *Beamish et al. 74047* (MASS), British Columbia; (PS-492), cult. M. *L. camtschatcensis* (L.) Schott (**PS-477**), *Penhallow s.n.* (MASS), Japan.

Genus: **Symplocarpus** Salisb. ex Nutt. Figures 131, 132.

Taxonomic Reference: Krause, 1908.

Published SEM Micrographs: S. foetidus (Grayum, 1986c); *S. nipponicus* (Iwanami et al., 1988).

Species Examined: 1/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm. EXINE SCULPTURING: *nonapertural exine* reticulate, the brochi reduced toward the aperture; *apertural exine* coarsely verrucate.

REMARKS: This genus has perhaps the most highly sculptured apertural exine in the Araceae.

Specimens Examined: S. foetidus (L.) Nutt. (**PS-22**), *Piper 53527* (MASS), Massachusetts; (PS-478), *Miner s.n.* (MASS), Massachusetts.

Genus: **Calla** L. Figures 133–136; 412.

Taxonomic Reference: Krause, 1908.

Published SEM Micrographs: C. palustris (Bobrov et al., 1983; Grayum, 1986c).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* diaperturate (see "Remarks"); *polarity* subisopolar. POLLEN SHAPE globose; *symmetry* isobisymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 23 μm (two samples each yielded this result). EXINE SCULPTURING: *nonapertural exine* foveolate, becoming rugulate immediately adjacent to the aperture membrane; *apertural exine* verrucate.

REMARKS: Pollen of *Calla palustris* has been variously described as dicolpate or -sulculate, inaperturate or monosulcate (see Erdtman, 1952; Thanikaimoni, 1969). At the light level, the grains appear clearly to be diaperturate; this term seems also to best describe the composite picture obtained from numerous SEM photos, although it is rarely possible to see both apertures of a single grain simultaneously.

Specimens Examined: C. palustris L. (**PS-13**), *Koch 5449* (MASS), Wisconsin; (**PS-144**), *Grayum 3081* (MASS), Massachusetts.

Genus: **Cyrtosperma** Griffith Figures 137, 138.

Taxonomic Reference: Hay, 1988a.

Published TEM Micrographs: C. hastatum (Van Campo & Lugardon, 1973).

Species Examined: 3/11.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 29 μm, range 28 (*C. merkusii*) 30 (*C.* sp. indet.) μm. EXINE SCULPTURING: *nonapertural exine* foveolate, becoming psilate near the aperture; *apertural exine* psilate. EXINE STRUCTURE: *nonapertural exine* with a thick foot layer and tectum interposed by a granular rather than columellar infratectal layer (Van Campo & Lugardon, 1973). EXINE STRATIFICATION with a thin layer of endexine present (Van Campo & Lugardon, 1973).

REMARKS: Hay (1988a) placed *Cyrtosperma hastatum* in synonymy (tentatively) under *C. macrotum*. He distinguished four informal "groups" in *Cyrtosperma* sens. str., of which at least two are represented below.

Specimens Examined: C. macrotum Becc. ex Engl.? (P-3619), *Nicolson 1457* (US), New Guinea. *C. merkusii* (Hassk.) Schott (**P-3618**), *Wong 367* (US), Yap. *C.* sp. indet. (PS-174), *Grayum 3082* (MASS), cult. MASS (orig. Papua New Guinea).

Genus: **Lasimorpha** Schott Figures 139, 140.

Taxonomic Reference: Hay, 1988a.

Published SEM Micrographs: L. senegalensis (Knecht, 1983a, b [as *Cyrtosperma senegalense*]).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 μm. EXINE SCULPTURING: *nonapertural exine* coarsely foveolate or subreticulate, psilate near the aperture; *apertural exine* appearing rugulate.

REMARKS: Pollen of *Lasimorpha* is rather smaller and has more coarsely foveolate exine than that of *Cyrtosperma*, from which this genus was recently (as "*Lasiomorpha*") resegregated (Hay, 1988a).

Specimen Examined: L. senegalensis Schott (**P-3620**), *Gossweiler 14156* (US), Angola.

Genus: **Anaphyllopsis** A. Hay Figures 141, 142; 443.

Taxonomic Reference: Hay, 1988b.

Species Examined: 1/3.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 31 μm. EXINE SCULPTURING: *nonapertural exine* foveolate; *apertural exine* appearing rugulate.

REMARKS: Pollen of this genus is slightly larger and has a more sculptured apertural exine than that of the *Cyrtosperma* species examined; *Anaphyllopsis* was recently segregated from the latter genus by Hay (1988b).

Specimen Examined: A. americana (Engl.) A. Hay (**PS-452**), *Wessels Boer 1223* (US), Surinam.

Genus: **Lasia** Lour. Figures 143, 144; 453.

Taxonomic Reference: Hay, 1988a.

Species Examined: 1/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 27 μm. EXINE SCULPTURING: *nonapertural exine* reticulate, abruptly psilate along the margins of the aperture; *apertural exine* psilate?

Specimen Examined: L. spinosa (L.) Thwaites (**P-3621**), *Nicolson 4245* (US), Ceylon [Sri Lanka].

Genus: **Anaphyllum** Schott Figures 145, 146.

Taxonomic References: Engler, 1911; Hay, 1992a.

Species Examined: 2/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 29 μm, range 25 (*A. beddomei*)–33 (*A. wightii*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate (*A. beddomei*) to reticulate (*A. wightii*), with elevated psilate regions in *A. wightii* var. ined. Free-standing columellae are visible within the brochi in *A. wightii*. Proximal face at least sometimes keeled; *apertural exine* psilate.

Specimens Examined: A. beddomei Engl. (PS-400), *Blasco s.n.* (K), India. *A. wightii* Schott (**PS-401**), *Fischer s.n.* (K), India. *A. wightii* Schott var. ined. (PS-402), *Sivadasan CU 19060* (K), India.

Genus: **Podolasia** N. E. Br. Figures 147, 148; 471.

Taxonomic Reference: Hay, 1988a.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 18 μm. EXINE SCULPTURING: *nonapertural exine* scabrate or verruculate, with minute foveolae or punctae on the surface between the verruculae; *apertural exine* not seen.

Specimen Examined: P. stipitata N. E. Br. (**P-3622**), *Nicolson 1366* (US), Sarawak.

Genus: **Urospatha** Schott Figures 149, 150.

Taxonomic References: Engler, 1911; Hay, 1992a.

Species Examined: 3/20.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 26 μm, range 25–28 μm. EXINE SCULPTURING: *nonapertural exine* subreticulate or subrugulate to reticulate, the brochi becoming smaller toward the aperture; *apertural exine* psilate.

REMARKS: Pollen of *Urospatha wurdackii*, a species that has been bandied about among three different genera (see discussion in Hay, 1992a), exhibits no taxonomically illuminating features. *Urospatha tuerckheimii* has generally been regarded as a synonym of *U. friedrichsthalii* Schott (T. Croat, pers. comm.); however, the latter name has been determined by Hay (1992a) to apply to a species of *Sagittaria* (Alismataceae). See also the remarks under *Cyrtosperma*.

Specimens Examined: U. grandis Schott (PS-293), *Hammel 8337* (DUKE), Costa Rica. *U. sagittifolia* (Rudge) Schott (**P-3624**), *Fonseca 173* (US), Brazil. *U. tuerckheimii* Engl. (P-3623), *Steyermark 39878* (US), Guatemala. *U. wurdackii* (Bunting) A. Hay (PS-487) [filed under "Araceae indet."], *Maguire 29328* (NY), Venezuela.

Genus: **Dracontioides** Engl. Figures 151, 152.

Taxonomic References: Engler, 1911; Hay, 1992a.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 23 μm. EXINE SCULPTURING: *nonapertural exine* subreticulate; *apertural exine* psilate?

Specimen Examined: D. desciscens (Schott) Engl. (**P-3625**), *Belem 3477* (US), Brazil.

Genus: **Dracontium** L. Figures 153–159; 402.

Taxonomic References: Engler, 1911; Bogner, 1985c; Hay, 1992a.

Published SEM Micrographs: D. dressleri (Croat, 1975); *D. margaretae* (Bogner, 1981c).

Species Examined: 5/18; *sections* 3/3.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 36 μm, range 29 (*D. asperum*)–43 (*D. pittieri*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate or foveolate-fossulate to subreticulate (*D. polyphyllum*). In *D. polyphyllum*, the brochi increase in size toward the center of the proximal face, which is keeled in this species; *apertural exine* rugulate or verruculate.

REMARKS: *Dracontium regelianum*, of section (until recently genus) *Echidnium*, is palynologically at home in *Dracontium*.

Specimens Examined: D. asperum K. Koch-D (**P-3626**), *Barrett s.n.* (US), cult. Washington (orig. Puerto Rico). *D. pittieri* Engl.-G (P-3550), *Allen 5318* (US), Costa Rica. *D. polyphyllum* L.-D (**PS-273**), *Bogner 1132* (M), cult. M. *D. regelianum* (Engl.) Bogner-E (**PS-191**), [*A.*] *Schott s.n.* (NY), Colombia. *D.* sp. indet.-I (P-3627), *Plowman & Davis 5045* (US), Peru. *Section Annotations:* D = *Dracontium*; E = *Echidnium* (Schott) Engl.; G = *Godwinia* (Seemann) Engl.; I = sect. indet.

Genus: **Pycnospatha** Thorel ex Gagnepain Figures 160, 161; 454.

Taxonomic References: Bogner, 1973a; Hay, 1992a.

Published SEM Micrographs: P. arietina (Bogner, 1973a).

Species Examined: 1/2.

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 34 μm. EXINE SCULPTURING: *nonapertural exine* subreticulate to rugulate, especially on the proximal face; free-standing columellae visible within the brochi, as in *Anaphyllum* and *Stylochaeton*; *apertural exine* psilate?

Specimen Examined: P. arietina Gagnepain (**PS-415**), *Bogner 395* (K), Thailand.

Genus: **Furtadoa** M. Hotta Figures 162, 163; 478.

Taxonomic References: Hotta, 1981, 1985.

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 17 μm. EXINE SCULPTURING virtually psilate.

Specimen Examined: F. sumatrensis M. Hotta (**PS-458**), *Hotta s.n.* (M), Sumatra [spirit collection].

Genus: **Homalomena** Schott Figures 164–169.

Taxonomic References: Engler, 1912; Furtado, 1939.

Published SEM Micrographs: H. speariae (Moffler & Bogner, 1984).

Species Examined: 8/147; *sections* 4/4.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar or subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 μm, range 12 (*H.* cf. *versteegii*)–31 (*H. speariae*) μm. Pollen of the neotropical section *Curmeria* (mean 28 μm, range 23–31 μm) averages larger than that of the Old World sections *Chamaecladon* (mean 15 μm) and *Homalomena* (mean 18 μm, range 12–24 μm). EXINE SCULPTURING perfectly psilate in most species; pollen of *H. wallisii* and *H. propinqua* is slightly textured (i.e., obscurely fossulate).

REMARKS: The pollen of *H.* cf. *versteegii* at 12 μm is the smallest yet measured in Araceae. *Homalomena* is here construed as including the monotypic *Diandriella* Engl., accommodated within sect. *Chamaecladon* (Bogner, 1985c); no pollen could be obtained from *Homalomena engleri* Bogner (formerly *Diandriella novoguineensis* Engl.).

Specimens Examined: H. cordata (Houtt.) Schott-H (P-3653), *Nicolson 1164* (US), Malaya. *H. hammelii* Croat & Grayum sp. ined.-Cu (PS-269), *Hammel 11429* (DUKE), Costa Rica. *H. lindenii* (Rodigas) Ridley-H (**P-3656**), *Bogner 464* (US), cult. M. *H. paucinervia* Ridley-Ch (PS-139), *Bogner 1448* (M), Sarawak. *H. propinqua* Schott-Cy (**P-3657**), *Sibat & Ilias S24732* (US), Sarawak. *H. speariae* Bogner & Moffler-Cu (**PS-268**), *Spear s.n.* (M), Colombia. *H.* cf. *versteegii* Engl.-H (P-3660), *Peterson J-1175* (US), cult. KEN (acc. no. 68845; orig. New Guinea). *H. wallisii* Regel-Cu (**PS-162**), cult. K (acc. no. 000-69.50430). *Section Annotations:* Ch = *Chamaecladon* Miq.; Cu = *Curmeria* (Linden & André) Engl.; Cy = *Cyrtocladon* Furtado; H = *Homalomena.*

Genus: **Aglaonema** Schott Figures 170–173.

Taxonomic Reference: Nicolson, 1969.

Species Examined: 2/21; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-elliptic to -elongate (*A. costatum*); *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 52 μm, range 37 (*A. simplex*)–67 (*A. costatum*) μm. The latter dimension was calculated directly from SEM micrographs, which would exaggerate the dimension on the downward side. EXINE SCULPTURING essentially psilate; obscurely textured—minutely verruculate or rugulate—however, this may be an artifact of critical-point drying.

REMARKS: The elongate, distinctively fusiform grains of *A. costatum*, in the ditypic section *Chamaecaulon*, differ considerably from those of *A. simplex*, a member of sect. *Aglaonema* (comprising the bulk of the genus). Whether or not this is significant must depend on an examination of additional species. Unexpected technical difficulty was experienced with this horticulturally familiar genus; samples of many species were processed, but only these two yielded pollen. Most plants in cultivation appear sterile and seem to produce no pollen.

Rao & Leong (1974) described pollen of *A. pictum* as "plicate," but most likely they were dealing with shriveled and/or sterile pollen.

Thanikaimoni (1969) described pollen of two species as "echinulate," and his light micrographs of pollen of *A. schottianum* show clearly spinose grains. These photos were taken at twice the magnification of the other *Aglaonema* shots and may depict fungal spores or foreign pollen. His other "echinulate" species (not illustrated) is *A. simplex*, shown here to be quite psilate.

Specimens Examined: A. costatum N. E. Br.-C (**P-3671**), *Belton 249* (US), cult. Oregon. *A. simplex* Blume-A (**PS-424**), *Bogner 1668* (M), cult. M; (P-3678), *Nicolson 1135* (US), cult. SING. *Section Annotations:* A = *Aglaonema*; C = *Chamaecaulon* Nicolson.

Genus: **Aglaodorum** Schott [Not illustrated.]

Taxonomic Reference: Engler, 1915.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 59 μm. EXINE SCULPTURING apparently psilate or verruculate.

REMARKS: The single polleniferous sample of this monotypic genus that could be obtained arrived too late for SEM study; all of the above information is thus based on observations of acetolyzed pollen under light microscopy.

Thanikaimoni (1969) figured pollen of *Aglaodorum* at the light level and described it as inaperturate and psilate.

Specimen Examined: A. griffithii Schott (PS-528), *Bogner 1672* (M), cult. M.

Genus: **Zantedeschia** Sprengel Figures 174, 175.

Taxonomic Reference: Letty, 1973.

Species Examined: 4/6.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar or subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm, range 31 (*Z. elliottiana*)–49 (*Z. aethiopica*) μm. EXINE SCULPTURING perfectly psilate to obscurely dimpled.

Specimens Examined: Z. aethiopica (L.) Sprengel (**P-3691**), *Nicolson 383* (US), cult. California. *Z. albomaculata* (Hook.) Baillon (PS-496), cult. MASS. *Z. elliottiana* Engl. (PS-25), *Torrey & Putala s.n.* (MASS), cult. MASS. *Z. rehmannii* Engl. (PS-26), *Torrey & Putala s.n.* (MASS), cult. MASS.

Genus: **Anubias** Schott Figures 176, 177.

Taxonomic References: Crusio, 1979, 1987.

Published SEM Micrographs: A. heterophylla (Crusio, 1979).

Species Examined: 3/8.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar to subisopolar. POLLEN SHAPE subspheroidal to spherical; *symmetry* bilateral to radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 24 μm, range 20 (*A. afzelii*)–31 (*A. heterophylla*) μm; pollen of *Anubias* shrinks considerably when processed for SEM, averaging only 12 μm (range 11–13 μm). EXINE SCULPTURING perfectly psilate to somewhat textured, i.e., obscurely verruculate and/or dimpled.

REMARKS: Thanikaimoni (1969) described pollen of *Anubias* as "echinulate" with faintly visible spines. His light micrographs of pollen of two species (including one of those investigated here) are unconvincing, however, and the objects interpreted as spines might well be debris adhering to the grains. Pollen of *A. heterophylla* illustrated by Crusio (1979) appears distinctly verrucate, as that of some species of *Culcasia* or *Nephthytis* sect. *Oligogynium*. Perhaps the material examined by me was misidentified.

Specimens Examined: A. afzelii Schott (**PS-234**), *Bogner 1569* (M), cult. M. *A. heterophylla* Engl. (P-3670), *Cambridge Congo Expedition 1959 #300* (US), Belgian Congo [Zaire]. *A. pynaertii* De Wild. (PS-520), cult. M.

Genus: **Schismatoglottis** Zoll. & Moritzi Figures 178–181.

Taxonomic References: Engler, 1912; Bunting, 1960a; Hotta, 1966.

Species Examined: 4/100; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to isopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 20 μm, range 15 (*S. homalomenoidea*)–26 (*S. spruceana*) μm; as in *Homalomena*, pollen of the neotropical species (sect. *Philonotion*) is considerably larger (mean 26 μm) than that of the Old World species (mean 17 μm, range 15–18 μm), though the sample size in both genera is too small to draw conclusions. EXINE SCULPTURING perfectly psilate in the Old World species studied; obscurely rugulate or verruculate in *S. spruceana*.

REMARKS: Hotta (1966) divided the Old World species (sect. *Schismatoglottis*) into five informal groups, three of which—Group A (*S. homalomenoidea*), Group B (*S. mayoana*), and Group E (*S. calyptrata*)—were represented in the present study.

Thanikaimoni (1969) claimed that the 14 species of this genus examined by him all had echinulate pollen, and his light micrographs of pollen of *S. forbesii* and *S. kurzii* bear this out. This is at variance with the present observations, and with what one would expect in this genus. It is possible that he has illustrated fungal spores, which are commonly yielded by improperly dried aroid spadices and frequently echinulate; however, it is inconceivable that these would have been encountered in 14 different samples. Erdtman (1963) published excellent light micrographs of pollen of an unidentified *Schismatoglottis*, and it is clearly psilate.

Specimens Examined: S. calyptrata (Roxb.) Schott-S (**P-3555**), *Peterson J-2356* (US), cult. KEN (acc. no. 701193; orig. New Guinea). *S. homalomenoidea* M. Hotta-S (PS-142), *Bogner 1607* (M), Sarawak. *S. mayoana* Bogner & M. Hotta-S (PS-379), *Bogner 1606* (M), Sarawak. *S. spruceana* (Schott) Bunting-P (**PS-485**), *Maguire et al. 36413* (NY), Venezuela. *Section Annotations:* P = *Philonotion* (Schott) Bunting; S = *Schismatoglottis*.

Genus: **Piptospatha** N. E. Br. Figures 182, 183.

Taxonomic References: Engler, 1912; Hotta, 1965.

Species Examined: 1/10; *sections* 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar or isopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small to medium-sized; mean 25 μm. EXINE SCULPTURING probably perfectly psilate, appearing dimpled as an artifact of processing.

REMARKS: No material of the monotypic sect. *Gamogyne* (N. E. Br.) M. Hotta could be obtained.

Specimen Examined: P. elongata (Engl.) N. E. Br. (**P-3664**) [sect. *Piptospatha*], *Mamit S35218* (US), Sarawak.

Genus: **Bucephalandra** Schott [Not illustrated.]

Taxonomic References: Bogner, 1980d, 1984b.

REMARKS: Three samples of this genus of two species were processed, and no pollen was recovered. J. Bogner (in litt.) reported that pollen of *B. motleyana* Schott is inaperturate and ellipsoid, with medium-sized (28–30 μm), and psilate exine sculpturing.

Genus: **Phymatarum** M. Hotta Figures 184, 185; 420.

Taxonomic Reference: Hotta, 1965.

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar or isopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean *19 μm. EXINE SCULPTURING perfectly psilate, or appearing dimpled probably as an artifact of treatment.

Specimen Examined: P. borneense M. Hotta (**PS-140**), *Bogner 1506* (M), Sarawak.

Genus: **Aridarum** Ridley Figures 186, 187.

Taxonomic References: Hotta, 1965; Bogner, 1979, 1981b, 1983a.

Published SEM Micrographs: A. annae (Bogner, 1981b); *A. nicolsonii* (Grayum, 1986c).

Species Examined: 3/7; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean *23 μm, range *16 (*A. purseglovei*)–*31 (*A. burttii*) μm. Pollen of *A. nicolsonii* (sect. *Aridarum*) averages 21 μm measured under the light microscope. EXINE SCULPTURING perfectly psilate to obscurely textured.

REMARKS: Bogner (1981b) described pollen of *A. annae* as "scabrate," obviously (judging from his photo) using that term differently from the way it is used here.

Specimens Examined: A. burttii Bogner & Nicolson-C (P-3666), *Chai S34072* (US), Sarawak. *A. nicolsonii* Bogner-A (**PS-150**), *Bogner 1421* (M), Sarawak. *A. purseglovei* (Furt.) M. Hotta-C (P-3668), *Sibat ak Luang S22534* (US), Sarawak. *Section Annotations:* A = *Aridarum*; C = *Caulescentia* M. Hotta.

Genus: **Heteroaridarum** M. Hotta [Not illustrated.]

Taxonomic Reference: Hotta, 1976.

REMARKS: Through the generosity of Paul Chai (SAR), staminate material from the holotype of *H. borneense* M. Hotta, sole species in this genus, was obtained, but it yielded no pollen.

Genus: **Hottarum** Bogner & Nicolson Figures 188, 189.

Taxonomic References: Bogner, 1978, 1984b; Bogner & Hotta, 1983.

Published SEM Micrographs: H. lucens (Bogner, 1983b); *H. sarikeense* (Bogner & Hotta, 1983).

Species Examined: 1/4.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean *14 μm. EXINE SCULPTURING perfectly psilate, or irregularly dimpled.

REMARKS: Bogner (1983b) described the pollen of *H. lucens* as "verrucose"; however, the "verrucae" appear to represent particles of debris adhering to an otherwise more or less psilate surface. Such debris is frequently seen on araceous pollen and may derive from tapetal material or perhaps even a stigmatic exudate.

Specimen Examined: H. sarikeense Bogner & M. Hotta (**PS-171**), *Bogner 1553* (M), Sarawak.

Genus: **Typhonodorum** Schott Figures 190, 191; 476.

Taxonomic References: Engler, 1915; Bogner, 1975.

Published SEM Micrographs: T. lindleyanum (Straka & Friedrich, 1984).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar or isopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 45 μm. EXINE SCULPTURING subverrucate, and obscurely foveolate or punctate.

REMARKS: Many grains show a peculiar groove or ridge that might be interpretable as a vestigial aperture.

Specimens Examined: T. lindleyanum Schott (PS-435), *Lorence DL 1472* (MO), Mauritius; (**PS-507**), *Bogner 1667* (M), cult. M.

Genus: **Peltandra** Raf. Figures 192–195.

Taxonomic References: Engler, 1915; Blackwell & Blackwell, 1974.

Published SEM Micrographs: P. alba, P. virginica (Grayum, 1986c).

Species Examined: 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to apolar. POLLEN SHAPE boat-shaped-elliptic (*P. Sagittifolia*) or spherical (*P. virginica*); *symmetry* bilateral or radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm, range 28 (*P. virginica*)–37 (*P. Sagittifolia*) μm. EXINE SCULPTURING spinose in *P. virginica*, the interspinal surfaces quite psilate; pollen of *P. Sagittifolia* is wholly devoid of spines and practically psilate. Thanikaimoni (1969) described pollen of this species as "reticulate"; this is no doubt due to the fact that the exine is pocked with shallow dimples or craters, the rims of which form a faintly reticulate pattern that is, however, not at all comparable to the columellate reticulum of *Lysichiton* and some species of *Anthurium*, for example.

REMARKS: According to the late H. E. Ahles (pers. comm.), there are but two species in the genus, as Engler (1915) originally indicated, though some sources specify as many as four. *Peltandra alba* Raf. is a synonym of *P. sagittifolia*.

Blackwell & Blackwell (1974) believed the genus to be monotypic, which is disproved by pollen characters alone; indeed, pollen grains of the two species examined differ so substantially that if the sporophyte generations were not known they would almost certainly be assigned to different genera.

Specimens Examined: P. sagittifolia (Michaux) Morong (**P-3689**), *Curtiss 6619* (US), Florida. *P. virginica* (L.) Schott & Endl. (**PS-20**), *Torrey & Livingston s.n.* (MASS), Massachusetts.

Genus: **Philodendron** Schott Figures 196–209; 474.

Taxonomic References: Krause, 1913; Bunting, 1986; Mayo, 1990, 1991.

Published SEM Micrographs: P. rugosum (Bogner & Bunting, 1983); *P. selloum* (Grayum, 1986c).

Species Examined: 25/700; *subgenera* 3/3; *sections* 8/10.

POLLEN TYPE: *aperture type* inaperturate; rarely, as in some grains of *P. rugosum* and *P. solimoesense*, sutures that may represent vestigial apertures occur on the presumed distal face. Pollen of *P. radiatum* splits open readily along the polar circumference; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong or occasionally (*P. radiatum*; subg. *Pteromischum*) -elongate, sometimes decidedly wedge-shaped in cross section (e.g., *P. callosum*); *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm, range 28 (*P. rhodoaxis*)–54 (*P. radiatum*) μm. The smallest pollen occurs in subg. *Pteromischum* (mean 29 μm, range 28–30 μm), the largest in sect. *Polytomium* (mean 54 μm) and subg. *Meconostigma* (mean 50 μm, range 47–53 μm). EXINE SCULPTURING: pollen of the majority of species (all those not mentioned specifically) is perfectly psilate; that of the remainder varies from minutely verruculate, scabrate or fossulate (*P. fragrantissimum, P. grandipes, P. hederaceum, P. linnaei, P. jodavisianum, P. pterotum*) to clearly punctate, subfossulate, subfoveolate, or subverrucate (*P. callosum, P. mexicanum, P. rugosum, P. wendlandii*). Pollen of *P. goeldii* is finely gemmate or verrucate, and that of *P. leal-costae* is densely and coarsely verrucate. *Philodendron* pollen is often uniformly rounded (i.e., circular in cross section), as in most psilate species, or it may be very obscurely (*P. linnaei, P. scandens*) to moderately keeled (*P. goeldii, P. hederaceum, P. leal-costae, P. jodavisianum, P. rugosum, P. wendlandii*) on what is presumably the proximal face, especially in species with more or less textured exine. In *P. mexicanum* and especially *P. callosum*, the keel is pronounced, and the boundary between the proximal and distal faces is sharply demarcated by an elevated ridge so that the grains are triangular in cross section. The two panels of the proximal face are somewhat differently textured from the distal face.

REMARKS: No satisfactory material was obtained of sect. *Camptogynium*, and none at all of sect. *Schizophyllum. Philodendron goeldii* was formerly included in the monotypic genus *Thaumatophyllum* (as *T. spruceanum* Schott). This and the recently described *P. leal-costae* are the only species in the genus with pedately compound leaves; palynologically they also show a resemblance and stand apart from the remainder of the genus. According to Thanikaimoni (1969), pollen of *T. spruceanum* is psilate; the verrucae are perhaps below the resolving power of the light microscope.

Roubik & Moreno (1991), working from light slides of apparently collapsed or split grains, characterized *Philodendron* pollen as monosulcate. Some of their interpretations for other aroid genera are similarly dubious.

Mayo (1991) synonymized *Philodendron selloum* K. Koch under *P. bipinnatifidum*.

Specimens Examined: P. aurantiifolium Schott-Pt (PS-

204), *Hammel 11147* (DUKE), Costa Rica. *P. bipinnatifidum* Schott ex Endl.-M (**P-3778**), *Crisci 81* (US), Argentina. *P. callosum* K. Krause-B (**PS-163**), *Kew Exped. to Roraima 242* (K), cult. K (acc. no. 174-78.01657; orig. Guyana). *P. fragrantissimum* (Hook.) Don-Ml (**PS-389**), *Grayum 2436* (DUKE), Costa Rica. *P. frits-wentii* Bunting-C (PS-164), cult. K (acc. no. 104-76.00785). *P. goeldii* G. Barroso-M (**PS-437**), [filed as *Thaumatophyllum spruceanum* Schott], *Steyermark & Bunting 102505* (MO), Venezuela. *P. grandipes* K. Krause-Ph (PS-390), *Hammel 9126* (DUKE), Costa Rica. *P. hederaceum* K. Krause-Mg (PS-491), *Killip & Smith 28378* (NY), Peru. *P. insigne* Schott-B (PS-165), *Storr 103* (K), cult. K (acc. no. 078-77.00667; orig. Brazil). *P. jodavisianum* Bunting-Ph (**PS-392**), *Grayum 3018* (DUKE), Costa Rica. *P. leal-costae* Mayo & G. Barroso-M (**PS-410**), *Harley et al. 19429* (K), Brazil. *P. mexicanum* Engl.-C (PS-21), *Pringle 8093* (MASS), Mexico. *P. pinnatifidum* (Jacq.) Kunth-Ml (P-3774), *Irwin et al. 10184* (US), Brazil. *P. pterotum* K. Koch & Aug.-Ph (PS-203), *Hammel 8150* (DUKE), Costa Rica. *P. ptarianum* Steyerm.-Pp (P-3775), *Agostini* 1574 (US), Venezuela. *P. radiatum* Schott-Po (**PS-111**), *Grayum 2534A* (DUKE), Costa Rica. *P. rhodoaxis* Bunting-Pt (**PS-113**), *Grayum 2438* (DUKE), Costa Rica. *P. rudgeanum* Schott-Pt (P-3776), *Irwin 47444* (US), Brazil. *P. rugosum* Bogner & Bunting-C (**PS-446**), *Bogner 1522* (M), Ecuador. *P. scandens* K. Koch & Sello-Ph (P-3777), *Gutiérrez V. & Barkley 17C460* (US), Colombia. *P. solimoesense* A. C. Smith vel aff.-M (P-3779), *Schultes & Cabrera 14605* (US), Colombia. *P. steyermarkii* Bunting-Pp (P-3780), *Steyermark et al. 113018* (US), Venezuela. *P. tenue* K. Koch-Ph (PS-212), *Hammel 11161* (DUKE), Costa Rica. *P. tripartitum* Schott-T (PS-112), *Sperry 982* (DUKE), Costa Rica. *P. tweedianum* Schott-M (P-3781), *Pedersen 2978* (US), Argentina. *P. wendlandii* Schott-B (**PS-367**), *Grayum 3270*, cult. MASS (orig. Costa Rica). *Section and Subgenus Annotations:* M = subg. *Meconostigma* (Schott) Engl.; Pt = subg. *Pteromischum* (Schott) Mayo; the remainder are sections of subg. *Philodendron:* B = *Baursia* Reichb.; C = *Calostigma* (Schott) Pfeiffer; Mg = *Macrogynium* Engl.; Ml = *Macrolonchium* Schott; Ph = *Philodendron*; Po = *Polytomium* Schott; Pp = *Philopsammos* Bunting; T = *Tritomophyllum* Schott.

Genus: **Dieffenbachia** Schott Figures 210–219; 423, 444.

Taxonomic Reference: Engler, 1915.

Species Examined: 9/50.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to virtually apolar. POLLEN SHAPE boat-shaped-elliptic to -oblong or nearly spherical; *symmetry* bilateral or radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE large; mean 79 μm, range 54 (*D. herthae*)–99 (*D. oerstedii*) μm. EXINE SCULPTURING almost perfectly psilate (*D. paludicola*, *D.* sp. indet.) to obscurely verruculate (*D. herthae*, *D. oerstedii*) and/or sparingly punctate-foveolate (*D. maculata*), to densely foveolate with scattered compound foveolae (*D. pittieri*, *D. seguine*). Pollen of *D. parlatorei* is coarsely tuberculate with rounded knobs, the surface of the latter being densely punctate-foveolate, whereas the surface of the exine between the knobs is merely obscurely verruculate.

REMARKS: This genus is in a state of taxonomic chaos. Little confidence is attached to any species identifications, hence it is possible that the same species may have been examined under more than one name.

The distinctive pollen of *D. parlatorei* is remarkably similar to that of *Syngonium triphyllum* and *S. standleyanum*. The compound foveolae seen in *D. pittieri* and *D. seguine* strikingly resemble those observed in *Chlorospatha croatiana*.

Specimens Examined: D. hammelii Croat & Grayum sp. ined. (PS-513), cult. DUKE (orig. Costa Rica). *D.* cf. *herthae* Diels (**P-3685**), *Wurdack 2131* (US), Peru. *D. maculata* (Lodd.) Don 'Amoena' (PS-425), *Bogner 1669* (M), cult. M. *D. oerstedii* Schott (P-3561), *Barlow s.n.* (US), Mexico. *D. paludicola* N. E. Br. ex Gleason (PS-489), *Tillett & Tillett 45316* (NY), British Guiana [Guyana]. *D. parlatorei* Linden & André (**P-3686**), *Hutchison 3189* (US), Colombia. *D. picta* Schott var. *barraquiniana* (Verschaff. & Lemaire) Engl. (**P-3688**), *Nicolson 1133* (US), cult. SING. *D. pittieri* Engl. & K. Krause? (**P-3683**), *Webster et al. 12624* (US), Honduras. *D. seguine* (Jacq.) Schott (P-3684), *Yuncker et al. 8551* (US), Honduras.

Genus: **Bognera** Mayo & Nicolson Figures 220, 221.

Taxonomic References: Madison, 1980; Nicolson, 1984.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 59 μm. EXINE SCULPTURING obscurely verruculate or scabrate, nearly psilate.

REMARKS: The species was described from the Amazon region as *Ulearum reconditum* Madison (1980); however, the consensus among workers in the field has been that it does not fit well into *Ulearum* or any other known genus, hence the new genus. *Bognera* probably belongs in tribe Dieffenbachieae of subfamily Philodendroideae (Bogner & Nicolson, 1991). Pollen morphology is consistent with the latter placement, and highly inimical to near alignment with *Ulearum*.

Specimen Examined: B. recondita (Madison) Mayo & Nicolson (**PS-202**), *Lleras et al. P17224* (US), Brazil.

Genus: **Cryptocoryne** Fischer ex Wydler Figures 222–224.

Taxonomic References: Engler, 1920; Rataj, 1975.

Species Examined: 6/50; *subgenera* 3/4 (sensu Rataj); *sections* 2/3 (sensu Engler).

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 34 μm, range 27 (*C. beckettii*)–42 (*C. spiralis*) μm. EXINE SCULPTURING perfectly psilate or obscurely dimpled. A vague to conspicuous median keel is discernible on what is presumably the proximal face, especially on the more elongate grains.

REMARKS: The exine is rather thick in this genus—usually 2–4 μm. No attempt was made to procure representative material for each of the 17 sections in Rataj's (1975) very finely subdivided classification of the genus; his subgenera are more or less equivalent to the sections of Engler (1920), and of authorities on other aroid genera. Arends et al. (1982) divided *Cryptocoryne* into 24 informal groups on the basis of geographic distribution, morphology, and chromosome numbers. The only significant infrageneric taxon for which polleniferous material was not obtainable is the monotypic sect. *Ciliatae* Engl., = subg. *Myrioblastus* (Wallich) Rataj, comprising *C. ciliata* (Roxb.) Fischer ex Wydler.

Specimens Examined: C. affinis N. E. Br.-S/B (**PS-189**), *van Balgooy 2598* (NY), Malaya. *C. albida* R. Parker-T/B (**P-3750**), *Jacobsen NJ 77-81* (US), Thailand. *C. beckettii* Thwaites ex Trimen-S/B (PS-251), cult. SUM. *C. cordata* Griffith-S/B (PS-190), *Larsen & Larsen 33077* (NY), Thailand. *C. spiralis* (Retz.) Fischer ex Wydler-C (PS-252), cult. SUM. *C. wendtii* de Wit-Sb/B (PS-237), *Bogner 470* (M), cult. M. *Section and Subgenus Annotations* (subgenus sensu Rataj/section sensu Engler): B = sect. *Bitubulosae* Engl.; C = *Cryptocoryne* [subg. *Suturina* Rataj/sect. *Unitubulosae* Engl.]; S = subg. *Submersina* Rataj; T = subg. *Terrestrina* Rataj.

Genus: **Lagenandra** Dalz. Figures 225, 226.

Taxonomic Reference: de Wit, 1978.

Species Examined: 2/14.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 36 μm, range 35–38 μm. EXINE SCULPTURING perfectly psilate or obscurely dimpled (probably as an artifact of treatment); a slight or moderate keel is apparent on the (presumably) proximal face.

REMARKS: The exine in *Lagenandra*, as in *Cryptocoryne*, is quite thick—up to 4.5 μm or more.

Specimens Examined: L. meeboldii (Engl.) C. Fischer (P-3574), *Saldanha 15277* (US), India. *L. toxicaria* Dalz.? (**P-3749**), *Nicolson 4262* (US), Ceylon [Sri Lanka].

Genus: **Filarum** Nicolson Figures 227, 228.

Taxonomic Reference: Nicolson, 1966.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small to medium-sized; mean *21 μm. EXINE SCULPTURING spinose, with very dense, narrow, delicate spines that are nodose in the middle.

REMARKS: Pollen of this genus is almost identical to that of *Ulearum*.

Specimen Examined: F. manserichense Nicolson (**P-3730**), *Mexia 6353* (US), Peru.

Genus: **Ulearum** Engl. Figures 229, 230.

Taxonomic Reference: Engler, 1920.

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 26 μm. EXINE SCULPTURING spinose, with many narrow, delicate spines that are somewhat nodose in the middle as in *Filarum*; surface between spines psilate.

REMARKS: *Ulearum reconditum* Madison (1980) is now considered best referable to its own genus (see *Bognera*).

Specimen Examined: U. sagittatum Engl. (**P-3711**), *Schunke V. 1239* (US), Peru.

Genus: **Zomicarpella** N. E. Br. [Not illustrated.]

Taxonomic Reference: Engler, 1920.

REMARKS: No polleniferous material was available from this ditypic genus. Pollen of *Zomicarpella amazonica* Bogner sp. ined. (*Bogner 1985*, M) studied by J. Bogner (in litt.) is inaperturate, spherical, 18–20 μm in diameter, and with spiny exine sculpturing; it is more similar to that of *Zomicarpa* spp. than to *Filarum* or *Ulearum*.

Genus: **Zomicarpa** Schott Figures 231, 232; 482.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: Z. riedeliana (Bogner, 1980b).

Species Examined: 2/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 32–33 μm. EXINE SCULPTURING spinose, with stout, broad-based, slightly uncinate spines (especially in *Z. steigeriana*). Exine surface between the spines densely and finely verruculate.

REMARKS: This genus stands apart somewhat from the rest of the Zomicarpeae palynologically and in several other features.

Specimens Examined: Z. riedeliana Schott (**PS-291**), *Bogner 1213* (M), Brazil. *Z. steigeriana* Schott? (PS-320), *Bento Pickel 2989* (A/GH), Brazil.

Genus: **Carlephyton** Jum. Figures 233, 234.

Taxonomic References: Bogner, 1972, 1975.

Published SEM Micrographs: C. glaucophyllum (Bogner, 1972).

Species Examined: 2/3; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 34 μm, range 33–35 μm. EXINE SCULPTURING spinose, the spines stout and broad-based in *C. diegoense*, relatively longer and narrower in *C. madagascariense.* Exine surface between the spines scabrate or verruculate, right up to the base of the spines in *C. diegoense*; in *C. madagascariense*, each spine is surrounded by a ± psilate halo. The spines appear articulate (contracted) basally in *C. diegoense.*

REMARKS: See "Remarks" under *Arophyton.* Bogner's (1972) photograph of pollen of *C. glaucophyllum* represents the earliest published SEM micrograph of araceous pollen known to me.

Specimens Examined: C. diegoense Bogner-P (PS-286), *Bogner 234* (M), Madagascar. *C. madagascariense* Jum.-C (**PS-285**), *Bogner 169* (M), Madagascar. *Section Annotations:* C = *Carlephyton*; P = *Pseudocolletogyne* Bogner.

Genus: **Colletogyne** Buchet Figures 235, 236; 422.

Taxonomic References: Bogner, 1972, 1975.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 39 μm. EXINE SCULPTURING spinose, with long, stout spines; surface of exine between spines obscurely verruculate. Spines slightly contracted basally.

REMARKS: See "Remarks" under *Arophyton.*

Specimen Examined: C. perrieri Buchet (**PS-135**), *Bogner 165* (M), Madagascar.

Genus: **Arophyton** Jum. Figures 237, 238.

Taxonomic References: Bogner, 1972, 1975.

Published SEM Micrographs: A. humbertii (Bogner, 1978).

Species Examined: 2/7.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 27 (*A. crassifolium*)–36 (*A. buchetii*) μm. EXINE SCULPTURING spinose, the spines stout and broad-based in *A. buchetii*, comparatively longer in *A. crassifolium*; spines varying much in size in *A. buchetii*, with quite small and intermediate sizes frequent. Surface of exine between spines verruculate or subfoveolate (*A. buchetii*), flush to the base of each spine. Spines slightly contracted basally.

REMARKS: Thanikaimoni (1969, 1972) suggested that spines of all three genera in the tribe Arophyteae are caducous and of two sizes. Whereas off-size spines are occasional (as in all spinose araceous pollen), only in *Arophyton buchetii* of this tribe are heteromorphic spines conspicuously developed. The spines may indeed be caducous with acetolysis, as also noted in the present study; however, the significance of this is unclear. Perhaps it relates to the articulate appearance of the spines in some species (see also *Callopsis*).

Specimens Examined: A. buchetii Bogner (**P-3564**), *Bogner 207* (US), Madagascar. *A. crassifolium* (Buchet) Bogner (PS-284), *Bogner 278* (M), Madagascar.

Genus: **Mangonia** Schott [Not illustrated.]

Taxonomic Reference: Bogner, 1973b.

Published SEM Micrographs: M. uruguaya (Bogner, 1973b).

REMARKS: No material of this ditypic and poorly known genus of subtropical South America was obtained. Bogner (1973b) described the pollen of *M. uruguaya* as inaperturate, ellipsoidal, 40 μm long, and with an "areolate" exine. Judging from his SEM micrograph, the exine sculpturing might better be described as smoothly verrucate or subrugulate, somewhat resembling that of *Gorgonidium vargasii* (Fig. 252).

Genus: **Asterostigma** Fischer & C. Meyer Figures 239–243; 418.

Taxonomic References: Engler, 1920; Crisci, 1971; Madison, 1976b.

Species Examined: 4/8; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic (*A. pavonii*) to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 36 μm, range 35–38 μm. EXINE SCULPTURING virtually psilate (*A. integrifolium, A. lividum, A. riedelianum*) or coarsely verrucate (*A. pavonii*). A weak to moderate keel is apparent on the presumably proximal face in the psilate-grained species.

REMARKS: Thanikaimoni (1969) described pollen of *A. lividum* as "scabrate" (it is almost perfectly psilate), and that of *A. vermicidum* as "reticulate." The latter species has since been transferred to *Gorgonidium*.

Specimens Examined: A. integrifolium Madison-A (PS-123), *Madison 7444* (SEL), Ecuador. *A. lividum* (Lodd.) Engl.-A (**PS-267**), *Bogner 1237* (M), Brazil; (P-3566), *Hatschbach 14711 & Guimarães 53* (US), Brazil. *A. pavonii* Schott-A (**PS-438**), *Croat 50968* (MO), Peru. *A. riedelianum* (Schott) Engl.-R (**PS-439**), *Harley 18565* (MO), Brazil. *Section Annotations:* A = *Asterostigma*; R = *Rhopalostigma* Schott.

Genus: **Synandrospadix** Engl. Figures 244, 245.

Taxonomic Reference: Engler, 1920.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 49 μm. EXINE SCULPTURING spinose, with blunt, stout, broad-based spines; surface of exine between spines finely verruculate. Spines appearing articulate basally.

REMARKS: Pollen of *Synandrospadix* is unique in the tribe Spathicarpeae in shape and ornamentation and is more like pollen of some species in Arophyteae (e.g., *Carlephyton diegoense*). Close alignment of the two tribes has occasionally been suggested (see discussion in Thanikaimoni, 1969).

Specimen Examined: S. vermitoxicus (Griseb.) Engl. (**P-3567**), *Cárdenas 4083* (US), Bolivia.

Genus: **Taccarum** Brongn. ex Schott Figures 246–249; 419, 477.

Taxonomic Reference: Bogner, 1989.

Published SEM Micrographs: T. warmingii (Bogner, 1989).

Species Examined: 2/5.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 63 μm, range 49 (*T. cardenasianum*)-76 (*T. weddellianum*) μm. EXINE SCULPTURING psilate (*T. warmingii*) to minutely scabrate or verruculate (*T. weddellianum*) to spinulose-spinose (*T. cardenasianum*). The spines of *T. cardenasianum* are most irregular, being usually quite small but occasionally large and stout or long and pointed, all on the same grain. An obscure keel is visible on the proximal face of *T. weddellianum*.

REMARKS: Spinose, boat-shaped pollen such as that of *T. cardenasianum* exhibits a combination of characteristics exceedingly rare in Araceae.

Specimens Examined: T. cardenasianum Bogner (**P-3565**), *Cárdenas 5630* (US), Bolivia. *T. weddellianum* Brongn. ex Schott (**PS-143**), *Bogner 458* (M), cult. M.

Genus: **Gorgonidium** Schott Figures 250–253; 469.

Taxonomic Reference: Bogner & Nicolson, 1988.

Published SEM Micrographs: G. vargasii, G. mirabile, G. vermicidum (Bogner & Nicolson, 1988).

Species Examined: 2/3.

POLLEN TYPE: *aperture type* inaperturate, or perhaps monosulcate in *G. vargasii* (see "Remarks"); *polarity* subisopolar to isopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 34 μm, range *27 (*G. vargasii*)-41 (*G. mirabile*) μm. EXINE SCULPTURING *G. mirabile:* verrucate, with small, hemispherical verrucae of variable size distributed unevenly over the surface of the grain; large, nearly psilate areas occur on some grains. *G. vargasii:* uniformly retiverrucate, i.e., with broad, flattened, irregularly lobed verrucae forming a vaguely reticulate pattern.

REMARKS: The three species of *Gorgonidium* differ considerably in pollen morphology. Whereas *G. mirabile* is clearly inaperturate, all three grains photographed from *G. vargasii* appear to be monosulcate. This feature, combined with the relatively small size of the pollen and the quasi-reticulate exine sculpturing, renders *G. vargasii* one of the most primitive species palynologically in the tribe Spathicarpeae. The monosulcate nature of *G. vargasii* pollen must be verified when better material becomes available. Pollen of *Gorgonidium vermicidum* illustrated by Bogner & Nicolson (1988) appears even more typically reticulate.

Specimens Examined: G. mirabile Schott (**P-3534**), *Nicolson 3390* (US), Bolivia. *G. vargasii* Bogner & Nicolson (**PS-459**), *Gay 1465* (US), Peru.

Genus: **Gearum** N. E. Br. [Not illustrated.]

Taxonomic Reference: Engler, 1920.

REMARKS: No material of this very poorly known monotypic Brazilian genus was available. Pollen of *G. brasiliense* N. E. Br. from the only recent collection (*Araujo Dias 41*) is described as inaperturate, ellipsoid, large (52–60 μm), and with psilate or obscurely verrucate exine sculpturing (J. Bogner, in litt.). SEM micrographs show a low but distinct raphe, possibly representing a vestigial aperture, along the distal face.

Genus: **Spathantheum** Schott Figures 254, 255.

Taxonomic Reference: Engler, 1920.
Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 54 μm. EXINE SCULPTURING nearly psilate (very obscurely verruculate); faint keel visible on proximal face.

Specimen Examined: S. orbignyanum Schott (**P-3568**), *Vargas C. 17507* (US), Peru.

Genus: **Spathicarpa** Hook. Figures 256, 257.

Taxonomic Reference: Engler, 1920.

Species Examined: 2/7.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-oblong to -elongate (*S. sagittifolia*); *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 48 μm, range 45 (*S. sagittifolia*)–51 (*S. hastifolia*) μm. EXINE SCULPTURING almost perfectly psilate; low median keel clearly visible on the proximal face.

REMARKS: Erdtman (1952) called attention to the "very distinct pollen type so far not found outside this genus." He did not specify what he felt to be unique about it; the pollen of *Spathicarpa* is indistinguishable by external morphology from that of many other Spathicarpeae, plus most species of *Philodendron*, and even *Cryptocoryne* and *Lagenandra*.

Specimens Examined: S. hastifolia Hook. (P-3458), *Krapovickas & Cristóbal 15945* (TEX), Argentina. *S. sagittifolia* Schott (**P-3729**), *Venturi 5765* (US), Argentina.

Genus: **Cercestis** Schott Figures 258–261.

Taxonomic References: Engler, 1911; Ntépé, 1981; Bogner, 1985c.

Published SEM Micrographs: C. mirabilis [as *Rhektophyllum mirabile*], *C. sagittatus* (Knecht, 1983a); *C. stigmaticus* (Knecht, 1983a, b).

Species Examined: 3/12.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to isopolar or apolar. POLLEN SHAPE boat-shaped-elliptic or -oblong to subspheroidal or spherical; *symmetry* bilateral or radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean *43 μm, range *36 (*C. congensis*) *52 (*C. mirabilis*) μm. EXINE SCULPTURING almost perfectly psilate (*C. mirabilis*) to obscurely fossulate-verrucate, with minute punctae scattered (*C. congensis*) or ± aggregated (*C. stigmaticus*). Proximal face with median keel, at least in *C. congensis*.

REMARKS: Knecht (1983a) described pollen of *C. sagittatus* as "scabrous." The exine in this genus is very thin and tears during sonication and/or acetolysis. The grains become so distorted that they cannot be measured accurately from light slides, so that measurements had to be made directly from SEM micrographs. Pollen of *C. mirabilis*, formerly in the now-defunct genus *Rhektophyllum*, agrees with that of other *Cercestis* species in this and other important features.

Specimens Examined: C. congensis Engl. (PS-407), *Linder 1795* (K), Zaire. *C. mirabilis* (N. E. Br.) Bogner (P-3646), *Louis 6110* (US), Belgian Congo [Zaire]; (**P-3647**), *Nicolson 1129* (US), cult. SING. *C. stigmaticus* N. E. Br. (**PS-408**), *Bogner 632* (K), Gabon.

Genus: **Nephthytis** Schott Figures 262, 263; 421.

Taxonomic Reference: Engler, 1911.

Published SEM Micrographs: N. afzelii (Knecht, 1983a; Grayum, 1986c); *N. hallaei* (Bogner, 1980c); *N. poissonii, N. swainei* (Knecht, 1983a).

Species Examined: 1/7; *sections* 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean *46 μm. EXINE SCULPTURING verrucate, with smooth, low, flat verrucae reminiscent of those of *Gorgonidium vargasii*.

REMARKS: As in *Cercestis*, the exine is too thin to permit accurate measurement from light slides. This was attempted, the mean value being 62 μm; however, most grains were abnormally elongated.

Nephthytis afzelii, the species examined in the present study, belongs in the monotypic sect. *Nephthytis*. No material was obtained from the larger sect. *Oligogynium*; however, Bogner (1980c) and Knecht (1983a) have described and illustrated pollen of three species in that section. In all cases, it is described as globular to ellipsoidal and verrucose; the verrucae are small and hemispherical, and unevenly distributed on the grain such that bare patches occur—all in all, quite similar to the situation in *Culcasia*.

Thanikaimoni (1969) described the verrucae of *N. hallaei* (as *Callopsis hallaei*) as caducous. He also spoke of "caducous verrucae" on the pollen of *N. afzelii*, and his photos (plus those of Knecht) seem to show something more substantial than was observed in the present study. If such were ever present in my material, they must have all fallen off at a very early stage.

Specimen Examined: N. afzelii Schott (**PS-240**) [sect. *Nephthytis*], *Knecht s.n.* (M), cult. M (orig. Ivory Coast).

Genus: **Anchomanes** Schott Figures 264–267.

Taxonomic Reference: Engler, 1911.

Species Examined: 3/10.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar or subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 64 µm, range 37 (*A. difformis*)–94 (*A. nigritianus*) µm. EXINE SCULPTURING quite psilate or obscurely verruculate; the exine is so thin that it is virtually impossible to prevent it wrinkling under the electron beam during photography.

REMARKS: Three samples—PS-152, PS-374, and P-3629—identified as *A. difformis* were studied. Of these, pollen of the last is so much larger than that of the other two that it is treated here as a different species.

Pollen of *A. nigritianus* is so similar to that of *Pseudohydrosme gabunensis* in its immense size and peculiar oblong shape that a close relationship between the two genera, as postulated by Bogner (pers. comm.), can hardly be doubted.

Specimens Examined: A. difformis (Blume) Engl. (**PS-152**), *Westwood s.n.* (K), cult. K (acc. no. 407-53.40702; orig. Ghana); (PS-374), *Bogner 1666* (M), cult. M. *A. nigritianus* Rendle (**PS-494**), *Bogner 640* (K), cult. K (acc. no. 104-76.00789; orig. Gabon). *A.* sp. indet. [filed as *A. difformis*] (**P-3629**), *Nicolson 982* (US), cult. BO.

Genus: **Pseudohydrosme** Engl. Figures 268, 269.

Taxonomic References: Engler, 1911; Bogner, 1981a.

Species Examined: 1/2; *sections* 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar or subisopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE very large; mean *106 µm, range *93–*114 µm. EXINE SCULPTURING psilate.

REMARKS: This West African genus comprises two rather different species, each known only from the type collections until the recent rediscovery of *P. gabunensis* (sect. *Pseudohydrosme*) by Bogner (1981a). No material was available of *P. buettneri* Engl., of sect. *Zyganthera* (N.E. Br.) Engl.

Pollen of *P. gabunensis* is the largest yet measured for any aroid species. The above measurements were calculated directly from SEM micrographs, a method that yields decidedly conservative results (see Discussion). Bogner (1981a) gave a range of 100–120 µm for pollen of this species (he did not mention the method of calculation).

Specimen Examined: P. gabunensis Engl., *Bogner 664* (K: **PS-414**; US: PS-455) (sect. *Pseudohydrosme*) Gabon.

Genus: **Montrichardia** Crüger Figures 270, 271.

Taxonomic Reference: Engler, 1911.

Published SEM Micrographs: M. arborescens (Grayum, 1986c).

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical to subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE large; mean 94 µm, range 92–96 µm. EXINE SCULPTURING psilate (wrinkling almost immediately under the electron beam due to the thin exine).

REMARKS: According to Thanikaimoni (1969), pollen of *M. arborescens* is "scabrous"; it is not (nor does it appear to be in his photos). Both Thanikaimoni (1969) and Erdtman (1952) noted that the exine in this species is extremely thin. This is true only in a relative sense, i.e., it is thin in proportion to the diameter of the pollen, which in this species is very large. The thickness of the exine of *M. arborescens* was measured at 1.2–1.8 µm in this study; many aroids have exine this thin; however, on pollen as small as that of many *Anthurium* species, for example, it may appear relatively thick.

Specimens Examined: M. arborescens (L.) Schott (PS-368), *Hammel 13133* (DUKE), Costa Rica; (**P-3553**), *Davidse & Llanos 5449* (US), Colombia.

Genus: **Callopsis** Engl. Figures 272–274; 483.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: C. volkensii (Bogner, 1980c).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 37 µm. EXINE SCULPTURING papillate, covered with stout, broad-based, blunt spines, each with a nipplelike apex; surface of exine between papillae obscurely verruculate. Spines appear articulate basally.

REMARKS: Pollen of this genus, especially in the form and articulate nature of the spines, recalls that of some Arophyteae (e.g., *Carlephyton*) and of *Synandrospadix*. Thanikaimoni (1969) described the spines of *Callopsis volkensii* pollen as "caducous," a term he used for the Arophyteae as well. He also referred to verrucate pollen in *C. hallaei*, a species since transferred to *Nephthytis*.

Specimens Examined: C. volkensii Engl. (**PS-159**), cult. K (acc. no. 367-78.03380); (P-3570), *Bogner 242* (US), Tanzania.

Genus: **Jasarum** Bunting Figures 275, 276; 424.

Taxonomic References: Bogner, 1985b; Madison, 1981.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 44 μm. EXINE SCULPTURING foveolate-reticulate.

REMARKS: The nature of the exine sculpturing as photographed for this species looks a little peculiar; it is possible that the material examined was slightly immature; however, this factor should not affect the gross details of sculpturing.

Specimens Examined: J. steyermarkii Bunting, *Tillett & Tillett 45527* (NY: PS-187; US: **P-3708**), British Guiana [Guyana].

Genus: **Scaphispatha** Brongn. ex Schott Figures 277, 278.

Taxonomic References: Bogner, 1980b; Madison, 1981.

Published SEM Micrographs: S. gracilis (Bogner, 1980b).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical to subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 45 μm. EXINE SCULPTURING coarsely verrucate with large, polygonal, flat-topped verrucae; surface of exine between the verrucae minutely verruculate, nearly psilate.

REMARKS: The exine sculpturing of *Scaphispatha* is unique in Araceae, perhaps most closely approached by that of *Colocasia indica* and *Amorphophallus konjac*.

Specimen Examined: S. gracilis Brongn. ex Schott (**P-3571**), *v. Luetzelburg 25984* (US), Brazil.

Genus: **Caladium** Vent. Figures 279–281.

Taxonomic Reference: Madison, 1981.

Published SEM Micrographs: C. bicolor (Grayum, 1986c); *C. paradoxum* (Mayo & Bogner, 1988).

Species Examined: 3/9.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 43 μm, range 38 (*C. lindenii*)-47 (*C. tuberosum*) μm. EXINE SCULPTURING perfectly psilate (*C. lindenii*) or obscurely dimpled or verruculate.

REMARKS: It was not possible to get a clear picture of polarity, symmetry, and pollen shape for *Caladium tuberosum* (until recently segregated in the monotypic genus *Aphyllarum*), since the material was not ideal and all of the grains had split open and were somewhat distorted. The pollen is presumably subspheroidal, as originally depicted by Moore (1895). According to Madison (1981), *C. tuberosum* combines certain features of *Caladium, Scaphispatha,* and *Xanthosoma*; palynologically, it is most similar to *Caladium*. Mayo & Bogner (1988) presented persuasive evidence that *Aphyllarum* should be submerged in the latter genus, and later furnished the indicated new combination (as Bogner & Mayo in Bogner & Nicolson, 1991: 45).

Specimens Examined: C. bicolor (Dryander) Vent. (**PS-107**), *Besse et al. 1030* (SEL), Ecuador. *C. lindenii* (André) Madison var. *sylvestre* Grayum (PS-248), *Hammel 11341* (DUKE), Panama. *C. tuberosum* (S. Moore) Bogner & Mayo (**PS-175**), *Sidney 1126 & Onishi 347* (NY), Brazil.

Genus: **Xanthosoma** Schott Figures 282–285; 429, 445.

Taxonomic References: Engler & Krause, 1920; Madison, 1981.

Published SEM Micrographs: X. plowmanii (Bogner, 1985d); *X. striatipes* (Grayum, 1986c).

Species Examined: 5/45; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to apolar. POLLEN SHAPE boat-shaped-elliptic or subspheroidal; *symmetry* bilateral or ± radiosymmetric. POLLEN-UNIT tetragonal to obscurely decussate tetrads. POLLEN SIZE individual grains medium-sized; mean 42 μm, range 35 (*X. viviparum*) 49 (*X. pedatum*) μm; tetrads: mean 76 μm, range 62–97 μm. EXINE SCULPTURING minutely punctate- or fossulate-verruculate.

REMARKS: Comparative difficulty was experienced in extracting satisfactory pollen in this genus. All species examined bear pollen in tetrads, but there is some circularity in this statement since Madison (1981) has virtually redefined the genus on this basis. Individual grains in tetrads of *Xanthosoma* tend to be more clearly demarcated externally than in those of *Chlorospatha*, in addition to being significantly larger; however, Bogner (1985d) reported grains of *X. plowmanii* as but 15–20 μm in diameter.

Thanikaimoni (1969) noted that pollen of *X. lindenii* is shed in monads; this species is now included in *Caladium* on the basis of this and other characters.

Specimens Examined: X. pedatum Hemsley-A (P-

3783), *Eyerdam & Beetle 8715* (US), Mexico. *X. pilosum* K. Koch & Aug.-X (**PS-398**), *Hammel 13248* (DUKE), Costa Rica. *X. striatipes* (Kunth) Madison-A (**PS-434**), *Huber 1986* (MO), Venezuela. *X. viviparum* Madison-I (PS-336), *Plowman et al. 6705* (A/GH), Peru. *X. weeksii* Madison-I (PS-173), *Bogner 1479* (M), cult. M. *Section Annotations:* A = *Acontias* (Schott) Engl.; I = sect. indet.; X = *Xanthosoma*.

Genus: **Chlorospatha** Engl. Figures 286–289; 455, 479.

Taxonomic References: Madison, 1981; Grayum, 1986b.

Published SEM Micrographs: C. corrugata (Bogner, 1985a).

Species Examined: 4/16.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT tetragonal tetrads. POLLEN SIZE individual grains medium-sized; mean 26 μm, range 24 (*C. hammeliana*)–29 (*C. castula*) μm; tetrads: mean 45 μm, range 41–48 μm. EXINE SCULPTURING quite psilate or very obscurely punctate (*C. corrugata*) to obscurely verruculate; pollen of *C. croatiana* is foveolate-reticulate, with psilate bands marking the boundaries between grains. Some of the foveolae are compound, just as in certain *Dieffenbachia* species.

REMARKS: See "Remarks" under *Xanthosoma*.

Specimens Examined: C. castula (Madison) Madison (PS-120), *Madison 2106* (SEL), Ecuador. *C. corrugata* Madison ex Bogner (**PS-134**), *Spear s.n.* (M), cult. M (orig. Colombia). *C. croatiana* Grayum subsp. *croatiana* (**PS-249**), *Hammel 11329* (DUKE), Panama. *C. hammeliana* Grayum & Croat (PS-525), *Hammel 13465* (MO), Panama.

Genus: **Syngonium** Schott Figures 290–303; 426, 428.

Taxonomic Reference: Croat, 1981.

Published SEM Micrographs: S. angustatum, S. schottianum (Grayum, 1986c).

Species Examined: 12/36; *sections* 3/4.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar to apolar. POLLEN SHAPE boat-shaped-oblong in *S. mauroanum* but more typically boat-shaped-elliptic to spherical or subspheroidal; *symmetry* bilateral to radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 48 μm, range 34 (*S. auritum*)–75 (*S. schottianum*) μm. Sect. *Cordatum* (*S. schottianum* the only member studied) has larger pollen than sect. *Syngonium* (mean 45 μm, range 34–64 (*S. neglectum*) μm). Pollen of *S. rayi* (sect. *Oblongatum*) averages 56 μm. EXINE SCULPTURING minutely fossulate or verruculate (*S. birdseyanum, S. mauroanum, S. rayi*); finely verrucate with subglobose, caducous verrucae (*S. schottianum*); narrowly rugulate and minutely scabrate (*S. neglectum*); spinose, with narrow, broad-based spines, minutely verruculate on the interspinal surface (*S. auritum*), or with long, stout spines, prominently scabrate on the interspinal surface (*S. angustatum, S. macrophyllum, S. podophyllum*); or tuberculate, with large rounded knobs that are foveolate-rugulate on the surface, with the intervening surface minutely verruculate and sparsely punctate (*S. standleyanum, S. triphyllum*).

REMARKS: The unusual diversity of exine sculpturing in *Syngonium* was first pointed out by Birdsey (1955), who documented this with light micrographs. The bulk of this diversity occurs within section *Syngonium*, which surpasses most aroid genera in this regard and is rivaled (or even outdone) only by *Amorphophallus* sect. *Conophallus*.

Specimens Examined: S. angustatum Schott-S (**P-3713**), *Arnoldo 2296* (US), Bonaire. *S. auritum* (L.) Schott-S (**P-3714**), *Leonard 3078* (US), Haiti. *S. birdseyanum* Croat & Grayum sp. ined-S (**PS-427**), *Grayum 2786* (DUKE), Costa Rica; *S. hoffmannii* Schott-S (P-3709), *Lewis et al. 226* (US), Panama. *S. macrophyllum* Engl.-S (PS-430), *Grayum 1836* (DUKE), Costa Rica. *S. mauroanum* Birdsey ex Bunting-S (P-3563), *Lewis et al. 1637* (US), Panama. *S. neglectum* Schott-S (**P-3710**), *Conzatti 3463* (US), Mexico. *S. podophyllum* (L.) Schott var. *podophyllum*-S (P-3462), *Rowell et al. 17M350* (TEX), Mexico. *S. podophyllum* Schott var. *peliocladum* (Schott) Croat-S (PS-371), *Hammel 13134* (DUKE), Costa Rica. *S. rayi* Croat & Grayum sp. ined.-O (PS-115), *Grayum 2985* (DUKE), Costa Rica. *S. schottianum* H. A. Wendl. ex Schott-C (**PS-205**), *Hammel 11150* (DUKE), Costa Rica. *S. standleyanum* Bunting-S (**PS-366**), *Hammel 13092* (DUKE), Costa Rica. *S. triphyllum* Birdsey ex Croat-S (PS-329), *Ray 11* (A/GH), Costa Rica. *Section Annotations:* C = *Cordatum* Croat; O = *Oblongatum* Croat; S = *Syngonium*.

Genus: **Steudnera** K. Koch Figures 304–307; 425, 461.

Taxonomic Reference: Engler & Krause, 1920.

Species Examined: 3/8.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 μm (*S. discolor*). EXINE SCULPTURING striate, the striae narrow, the furrows broad and shallow; no evidence of columellae. The striae are in the "baseball" pattern of *Holochlamys*.

REMARKS: Thanikaimoni (1969) assigned *Steudnera* pollen to his "echinulate" category, but there is no evidence that he looked at material of this genus.

According to Li (1979), *S. henryana* Engl. is a synonym of *S. colocasiifolia* K. Koch.

Specimens Examined: S. capitellata Hook. f. (P-3695), *Shaik Mokim s.n.* (US), Burma. *S. discolor* W. Bull (**PS-199**), *Bogner 1582* (M), cult. M. *S. henryana* Engl. (P-3694), *Henry 11986A* (US), China.

Genus: **Colocasia** Schott Figures 308–313; 462, 484.

Taxonomic Reference: Engler & Krause, 1920.

Published SEM Micrographs: C. esculenta (Straka & Friedrich, 1984; Grayum, 1986c).

Species Examined: 3/8; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar or apolar. POLLEN SHAPE boat-shaped-oblong (*C. fallax*) to -elliptic (*C. indica*) or spherical to subspheroidal (*C. esculenta*); *symmetry* bilateral or radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small to medium-sized; mean 25 μm, range 25–26 μm. EXINE SCULPTURING finely striate (*C. fallax*) to coarsely swirling-fossulate (*C. indica*) or fossulate-spinose (*C. esculenta*). The markedly tenuous striae of *C. fallax* are closely approximate and extend from one end to the other in the parallel "football" pattern of *Spathiphyllum* (but without psilate patches at the ends as in that genus). The long, pointed, broad-based spines of *C. esculenta* are borne singly or in small groups on plates or "islands" formed by a coarse network of fossulae. The pollen of *C. indica* appears to link these two extremes.

REMARKS: For such a small genus, the pollen of *Colocasia* is remarkably diverse, amply illustrating the importance of studying as broad a range of species as possible.

Colocasia esculenta is the only species of Araceae in which pollen was observed still in the tetrad stage (apart from genera that shed pollen in permanent tetrads). Only one tetrad of *C. esculenta* was observed, which was decussate. Jos & Vijaya Bai (1978) observed 10% of pollen of this species in dyads, with occasional tetrads.

Straka & Friedrich (1984) stated, incorrectly, that pollen of *C. esculenta* is monosulcate; the grains they illustrated are merely collapsed. This is confirmed by recent observations of S. G. Haberle (in litt.).

Li (1979) listed *C. indica* Engl. in synonymy under *C. gigantea* (Blume) Hook. f.

Specimens Examined: C. esculenta (L.) Schott-Co (**PS-14**), *Taylor 32* (MASS), Dominica; (P-3705), *Nicolson 4247* (US), Ceylon [Sri Lanka]. *C. fallax* Schott-Co (**PS-136**), *Bogner 1139* (M), India. *C. indica* (Lour.) Hassk.-Ca (**PS-160**), cult. K (acc. no. 367-79.03392). *Section Annotations:* Ca = *Caulescentes* Engl.; Co = *Colocasia*.

Genus: **Gonatanthus** Klotzsch Figures 314, 315; 485.

Taxonomic Reference: Engler & Krause, 1920.

Published SEM Micrographs: G. sarmentosus (Kuprianova & Tarasevich, 1984; detail only).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm. EXINE SCULPTURING spinose, with long, sharp spines; interspinal surface prominently scabrate or spinulose.

REMARKS: Pollen of *Gonatanthus sarmentosus* is nearly identical to that of *Remusatia vivipara*, differing principally in its somewhat smaller and more densely aggregated spinules.

Specimen Examined: G. sarmentosus Klotzsch (**P-3696**), *Stewart 14852* (US), N. W. Himalayas.

Genus: **Remusatia** Schott Figures 316, 317.

Taxonomic Reference: Engler & Krause, 1920.

Published SEM Micrographs: R. vivipara (Straka & Friedrich, 1984).

Species Examined: 1/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm. EXINE SCULPTURING spinose with long, sharp spines; interspinal surface spinulose.

REMARKS: See "Remarks" under *Gonatanthus*.

Specimen Examined: R. vivipara (Roxb.) Schott (**P-3562**), *Ramamoorthy HFP1385* (US), India.

Genus: **Hapaline** Schott Figures 318, 319.

Taxonomic Reference: Engler & Krause, 1920.

Published SEM Micrographs: H. brownii (Barthlott, 1985, detail only; Bogner, 1987).

Species Examined: 1/5.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 40 μm. EXINE SCULPTURING rather densely spinose with broad-based, sharp spines. Interspinal surface psilate or nearly so.

Specimen Examined: H. brownii Hook. f. (**PS-137**), *Burtt & Woods 1771* (M), Malaya.

Genus: **Alocasia** (Schott) Don Figures 320–325; 427.

Taxonomic References: Engler & Krause, 1920; Nicolson, 1968a; Hay, 1989, 1990; Hay & Wise, 1991.

Species Examined: 6/72; sections 2/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical to subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 35 μm, range 31 (*A. atropurpurea*) 39 (*A. cuprea*) μm. EXINE SCULPTURING spinose, the spines ranging from short, stout, and blunt (*A. lancifolia*) to long and pointed (*A. portei*), and from numerous (*A. atropurpurea, A. cucullata*) to rather few (*A. portei*). Interspinal surface virtually psilate (*A. portei*) to minutely fossulate (*A. lauterbachiana*), verruculate (*A. hollrungii*) or subscabrate (*A. cuprea*), with the ornamentation extending onto at least the basal half of the spines.

REMARKS: No material was obtained from the monotypic Australian sect. *Ozarum* A. Hay (1989). The two polytypic sections are evidently artificial (Hay & Wise, 1991), but have not been revised.

Hay (1990) and Hay & Wise (1991) have submerged *Xenophya* (represented here by *Alocasia lauterbachiana*) in *Alocasia*, aligning it with species included by Engler & Krause (1920) in sect. *Alocasia*. *Xenophya* is easily accommodated in *Alocasia* from the palynological standpoint.

Specimens Examined: A. atropurpurea Engl.-A (P-3698), *Field & Loew 65* (US), Okinawa. *A. cucullata* (Lour.) Don-A (**PS-460**), cult. MASS; (P-3699), *Nicolson 1046* (US), Malaya. *A. cuprea* K. Koch-E (PS-462), cult. DUKE (acc. no. 66004). *A. hollrungii* Engl.-A (P-3702), *Nicolson 1455* (US), New Guinea. *A. lancifolia* Engl.-A (P-3703), *Peterson J-1407* (US), cult. KEN (acc. no. 701267; orig. New Guinea). *A. lauterbachiana* (Engl.) A. Hay-A (**P-3704**), *Nicolson 1395* (US), cult. LAE. *A. portei* Schott-I (**PS-373**), *Bogner s.n.* (M), cult. M. *Section Annotations:* A = *Alocasia*; E = *Ensolenanthe* (Schott) Engl.; I = sect. indet.

Genus: **Stylochaeton** Lepr. Figures 326–332; 403, 430, 446, 456.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: S. crassispathus (Bogner, 1984a).

Species Examined: 3/21; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate or monosulcoidate (see "Remarks"); *polarity* subisopolar or heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE large; mean 53 μm, range 43 (*S. zenkeri*) 58 (*S. natalensis*) μm. Pollen of sect. *Spirogyne* (mean 57 μm) averages larger than that of sect. *Stylochaeton* (mean 43 μm); however, the sample size is very small. EXINE SCULPTURING foveolate-reticulate (*S. zenkeri*) or subreticulate, the muri often appearing beaded; free-standing columellae visible within the brochi (at least in *S. zenkeri*); proximal face obscurely keeled (at least in *S. natalensis*).

REMARKS: Pollen of *S. lancifolius* (Thanikaimoni, 1969) and *S. crassispathus* (Bogner, 1984a) has been described as "inaperturate"; both are in sect. *Stylochaeton*. Erdtman (1952) observed that pollen of *S. hennigii* (sect. *Spirogyne*) was "nonaperturate or provided with a small ulceroid or sulcoid aperture." All of these authors may have been correct; in the present investigation, some grains of both species in sect. *Spirogyne* were found to exhibit what can only be interpreted as a vestigial aperture, exactly where it would be expected, on the presumably distal face (the more rounded face opposite the keeled "proximal" face). Other grains of the same species were seen in which the distal face clearly lacked any traces of such a vestige; moreover, no evidence of vestigial apertures was ever seen in pollen of *S. zenkeri* (sect. *Stylochaeton*). Pollen of the last-mentioned species also differs from that of the species of sect. *Spirogyne* examined in being smaller, rounder (less prominently boat-shaped), and in having a foveolate-reticulate (i.e., with rounder brochi) rather than rugulate-reticulate exine. Whether these differences hold up throughout the two sections must await further studies. If so, sect. *Spirogyne* must be considered more primitive palynologically, as it is in its spiral (rather than whorled) arrangement of female flowers.

If vestigial apertures were being sought in the Araceae, *Stylochaeton*—the only genus in the family with boat-shaped, reticulate, inaperturate pollen—is exactly where one should think to look first.

Light slides were found not to be useful in verifying the semiaperturate nature of *Stylochaeton* pollen; the exine in this genus is quite thin (contrary to the statement of Erdtman), tearing and invaginating so that it is impossible to distinguish apertures from chance rents or folds.

I doubt the statement of Thanikaimoni (1969) that *Stylochaeton* pollen is intectate; TEM studies are needed.

Specimens Examined: S. bogneri Mayo-Sp (**PS-243**), *Bogner 148* (K), Tanzania. *S. natalensis* Schott-Sp (**P-3717**), *Huttleston 2255* (US), cult. KEN (acc. no. 66664). *S. zenkeri* Engl.-S (**PS-244**), *Bogner 631* (M), cult. M (orig. Gabon). *Section Annotations:* S = *Stylochaeton*; Sp = *Spirogyne* Engl.

Genus: **Arum** L. Figures 333–335.

Taxonomic Reference: Boyce, 1989.

Published SEM Micrographs: A. alpinum (Hesse, 1983; Bedalov, 1985; Bedalov & Hesse, 1989); *A. creticum* (Hesse, 1983); *A. dioscoridis* (Bedalov, 1985; Grayum, 1986c); *A. palaestinum* (Hesse, 1983; Bedalov & Hesse, 1989); *A. pictum, A. nigrum, A. maculatum, A. orientale* subsp. *orientale, A. o.* subsp. *longispatha, A. italicum* (Bedalov, 1985); *A. orientale* subsp. *engleri, A. apulum, A. conophalloides, A. korolkowii, A. jacquemontii* (Bedalov & Hesse, 1989).

Published TEM Micrographs: A. italicum (Pacini & Juniper, 1983; Pacini, 1990; late microspore stage); *A. maculatum* (Hesse, 1980, 1983).

Species Examined: 5/24; *subgenera* 2/2; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 29 (*A. maculatum*)–34 (*A. palaestinum*) μm. EXINE SCULPTURING usually spinose, with short, stoutly conical spines; interspinal surface finely verruculate or subfossulate and sparsely spinulose. *Arum korolkowii* has uniformly verruculate pollen without spines (Bedalov & Hesse, 1989). EXINE STRUCTURE the exine of *A. maculatum* possesses neither columellae nor a tectum (Hesse, 1980). In late microspores of *A. italicum*, the exine is described as homogeneous, whereas the spines are granular; there is an evident interface between the two (Pacini & Juniper, 1983).

REMARKS: Boyce (1989) divided sect. *Dioscoridea* into six subsections, all but one (subsect. *Hygrophila*) of which have now been investigated palynologically.

Specimens Examined: A. dioscoridis Sibth. & Smith-D (**P-3735**), *Nicolson 1737* (US), Lebanon. *A. italicum* Miller-A (PS-509), cult. M. (orig. Yugoslavia); (P-3733), *Lassimonne 758* (US), France. *A. maculatum* L.-A (**PS-11**), *Price s.n.* (MASS), Wales; (PS-503), *Bogner 584* (M), Bavaria; (P-3734), *West 1211* (US), England. *A. palaestinum* Boiss.-D (P-3736), *Baggley 30* (US), Jordan. *A. pictum* L. f.-G (PS-188), *Stefani s.n.* (NY), Corsica. *Section and Subgenus Annotations:* G = subg. *Gymnomesium* (Schott) Engl.; the remainder are sections of subg. *Arum:* A = *Arum*; D = *Dioscoridea* (Engl.) P. C. Boyce.

Genus: **Dracunculus** Hill Figures 336, 337.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: D. vulgaris (Dahlgren & Clifford, 1982 [see "Remarks"]; Grayum, 1986c).

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to isopolar. POLLEN SHAPE boat-shaped-elliptic or subspheroidal; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 45 μm. EXINE SCULPTURING verrucate, the verrucae smoothly flattened and closely approximate—much like *Nephthytis afzelii*, but the verrucae in *D. vulgaris* are more discrete (i.e., contracted basally). The surface of the verrucae and of the exine between them is minutely verruculate or dimpled. A weak median keel is visible on the (presumably) proximal face.

REMARKS: As is the case with some *Amorphophallus* species, *D. vulgaris* produces a certain percentage of sterile grains (they show no nuclei when stained with acetocarmine) that are smaller and more oblong than the typical pollen and are nearly psilate rather than verrucate. Evidently, one of these sterile grains is depicted by Dahlgren & Clifford (1982).

Specimens Examined: D. vulgaris Schott (**PS-510**), cult. Gloucestershire, England; (P-3737), *Gay s.n.* (US).

Genus: **Helicodiceros** Schott [Not illustrated.]

Taxonomic Reference: Engler, 1920.

REMARKS: No satisfactory material of this monotypic Mediterranean genus could be obtained, although it is sometimes cultivated. According to Thanikaimoni (1969), the pollen is inaperturate and "echinulate" (spinose); judging from his photos, it is also spherical, and the spines are rather short. *Helicodiceros* is sometimes included in *Dracunculus* (e.g., by Prime & Webb, 1980); pollen morphology does not support this.

Genus: **Theriophonum** Blume Figures 338, 339; 486.

Taxonomic Reference: Sivadasan & Nicolson, 1982.

Species Examined: 1/5.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean *25 μm. EXINE SCULPTURING spinose, the spines relatively long and slender; interspinal exine surface densely foveolate.

REMARKS: Engler (1920) distinguished two sections in this genus; Sivadasan & Nicolson (1982) made use of no infrageneric classification.

Specimen Examined: T. infaustum N. E. Br. (**PS-417**), *Barnes s.n.* (K), India.

Genus: **Lazarum** A. Hay [Not illustrated.]

Taxonomic Reference: Hay, 1992b.

Pollen of *L. mirabile* A. Hay (*Gallen 3*), the sole species of this Australian genus of subtribe Arinae, is inaperturate, shed in monads, medium-sized (34–40 μm) and with spinose exine sculpturing (Hay, 1992b). Vestiges of a reticulum are evident between the spines.

Genus: **Typhonium** Schott Figures 340–345; 435, 475.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: T. blumei, T. trilobatum (Grayum, 1986c).

Species Examined: 4/25; *sections* 2/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm, range 28 (*T. blumei*)–36 (*T.*

trilobatum) μm. EXINE SCULPTURING spinose, with numerous fairly long, sharp spines; interspinal exine surface minutely verruculate. *Typhonium giraldii* (the only member of sect. *Heterostalis* examined) has somewhat sparser spines. Pollen of *T. trilobatum* is very different, being densely verrucate, with small, psilate, hemispherical verrucae; the interspinal surface is psilate in this species.

REMARKS: Pollen of *T. trilobatum*, in addition to being verrucate, is also larger and less spherical than that of the other species. Such extreme palynological variation in a group that is otherwise very uniform (Nicolson & Sivadasan, 1981) suggests that pollen morphology may prove to be an important character at the species level in *Typhonium*.

Li (1979) listed *T. giraldii* in synonymy under *T. giganteum* Engl.

Specimens Examined: T. blumei Nicolson & Sivad. (**PS-380**), cult. M; (P-3739), *Hu 10095* (US), Hong Kong. *T. giraldii* (Baroni) Engl.-H (**PS-419**), cult. K. *T. roxburghii* Schott-T (PS-325), *Curran 324* (A/GH), Brazil; (PS-420), cult. K; (P-3740), *Nicolson 4152* (US), cult. India. *T. trilobatum* (L.) Schott-T (**PS-324**), *Kostermans 1043* (A/GH), Siam [Thailand]; (PS-450), *Hay 2045* (K), Malaya. *Section Annotations:* H = *Heterostalis* (Schott) Engl.; T = *Typhonium*.

Genus: **Sauromatum** Schott Figures 346, 350.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: S. guttatum (Meeuse et al., 1984).

Species Examined: 1/2.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 μm. EXINE SCULPTURING spinose, with stout, pointed spines; interspinal surface obscurely verruculate, nearly psilate.

Specimen Examined: S. venosum (Aiton) Schott (**PS-242**), *Bogner 1602* (M), N. India.

Genus: **Eminium** (Blume) Schott Figures 347, 351.

Taxonomic References: Riedl, 1969, 1980.

Species Examined: 2/6.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 44 μm (*E. intortum*). EXINE SCULPTURING spinose, the spines quite short and blunt (*E. intortum*) or longer and more pointed (*E. lehmannii*), broad-based and appearing articulate (contracted basally). Interspinal surface obscurely (*E. intortum*) or prominently (*E. lehmannii*) verruculate.

Specimens Examined: E. intortum (Sol.) Kuntze (**P-3573**), *Nicolson 1743* (US), Lebanon. *E. lehmannii* (Bunge) Kuntze (P-3742), *Awdezew & Awdezew s.n.* (US), U.S.S.R.

Genus: **Biarum** Schott Figures 348, 349, 352, 353.

Taxonomic References: Engler, 1920; Riedl, 1980.

Published SEM Micrographs: B. arundanum, B. galianii, B. carratracense, B. dispar (Talavera, 1976; according to Riedl (1980), the first two are synonymous with *B. tenuifolium*, the second two with *B. bovei* Blume (subg. *Ischarum*)); *B. ditschianum* (Bogner & Boyce, 1989).

Species Examined: 3/21; *subgenera* 3/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical to subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 30 μm (*B. tenuifolium*); *B. spruneri* (subg. *Cyllenium*) may be significantly smaller, averaging 16 μm as calculated from SEM micrographs. Talavera (1976) indicated a size range for pollen of this genus of 26–33 μm (*B. arundanum*) to 45–56 μm (*B. carratracense*). EXINE SCULPTURING spinose, the spines short and very broad (*B. tenuifolium*) to more slender, broad-based; interspinal exine obscurely (*B. spruneri, B. olivieri*) or distinctly (*B. tenuifolium*) verruculate.

Specimens Examined: B. olivieri Blume-I (PS-327), *Samaritani 3213* (A/GH), Egypt. *B. spruneri* Boiss.-C (**PS-404**), *Hodgkin s.n.* (K), Greece. *B. tenuifolium* Schott-B (**PS-326**), *Spencer s.n.* (A/GH), Sicily. *Subgenus Annotations:* B = *Biarum*; C = *Cyllenium* (Schott) Engl.; I = *Ischarum* (Blume) Engl.

Genus: **Arisaema** C. Martius Figures 354–356; 488.

Taxonomic References: Hara, 1971; Ohashi & Murata, 1980; Murata, 1984, 1990, 1991.

Published SEM Micrographs: A. triphyllum (Zavada, 1983; Murata, 1984); *A. amurense* (Ohashi & Murata, 1980; Ohashi et al., 1983; Oh et al., 1990); *A. ternatipartitum, A. heterocephalum, A. serratum* (Ohashi & Murata, 1980; Ohashi et al., 1983); *A. abei, A. aprile, A. cucullatum, A. ishizuchiense, A. iyoanum, A. kawashimae, A. kishidae, A. kiushianum, A. kuratae, A. longipedunculatum, A. maximowiczii, A. monophyllum, A. nikoense, A. ogatae, A. sazensoo, A. sikokianum, A. tashiroi, A. tosaense, A. undulatifolium, A. yamatense* (Ohashi et al., 1983); *A. heterophyllum, A. negishii* (Ohashi et al., 1983; Oh et al., 1990); *A. franchetianum* (Kuprianova & Tarasevich, 1984; Murata, 1984); *A. consanguineum, A. costatum, A. dracontium, A. exappendiculatum, A. flavum, A. nepenthoides, A. rhizomatum, A. utile, A. wrayi, A. yunnanense*

(Murata, 1984); *A. japonicum* (Iwanami et al., 1988); *A. peninsulae, A. ringens, A. robustum, A. takesimense* (Oh et al., 1990).

Published TEM Micrographs: A. amurense, A. heterophyllum, A. peninsulae, A. ringens (Oh et al., 1990); *A. serratum* (Ohashi et al., 1983); *A. triphyllum* (Zavada, 1983).

Species Examined: 20/150; *sections* 9/11.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 22 μm, range 17 (*A. speciosum*)–39 (*A. flavum*) μm. Pollen of sects. *Sinarisaema, Tortuosa, Tenuipistillata, Arisaema,* and *Trisecta* averages 21 μm or less; the larger grains occur in sects. *Fimbriata* (mean 27 μm), *Franchetiana* (mean 25 μm), and *Dochafa* (mean 39 μm). EXINE SCULPTURING spinose, the spines mostly stoutly conical and rather blunt (e.g., *A. fimbriatum, A. consanguineum, A. macrospathum, A. nepenthoides, A. ringens*) to sharp-pointed (e.g., *A. yunnanense, A. murrayi, A. dracontium, A. wallichianum, A. tortuosum, A. flavum*). Interspinal exine surface typically psilate, obscurely verruculate in *A. candidissimum* and *A. franchetianum,* distinctly so in *A. dracontium.* Low, off-size spines are occasional in most species, but only in *A. speciosum, A. dracontium, A. tortuosum,* and to a lesser extent *A. yunnanense, A. murrayi,* and *A. amurense,* are they sufficiently frequent to describe the interspinal surface as sparingly spinulose or verrucate. According to Oh et al. (1990), some pollen grains of *Arisaema amurense* have perfectly psilate exine. EXINE STRUCTURE: According to Zavada (1983) the pollen wall of *A. triphyllum* is tectate and imperforate, with a "spongy" infratectal layer; however, both Ohashi et al. (1983) and Oh et al. (1990) described pollen of this genus as intectate, interpreting the spongy layer as endexine. I suspect that Zavada's analysis is the correct one, for reasons discussed in a later section. EXINE STRATIFICATION: There is "no footlayer or endexine evident" in pollen of *A. triphyllum* (Zavada, 1983); as noted above, however, both Ohashi et al. (1983) and Oh et al. (1990) described a thick endexine in pollen of *Arisaema.*

REMARKS: The sectional classification of Engler (1920) was substantially overhauled by Hara (1971), whose system is adopted herein, for the most part. The infrageneric classification of *Arisaema* remains unsettled, however, and probably will not stabilize until a worldwide monograph is available. Li (1979) adopted Hara's system for the Chinese species, but later (Li, 1980) dispensed with sect. *Flagellarisaema* (Nakai) H. Hara, as did Ohashi & Murata (1980) in their revision of the Japanese species (submerging it in sect. *Tortuosa*). The latter authors resurrected sect. *Clavata* Engl., restoring Hara's original total of 13 sections. Murata (1984, 1991) has now reduced that number to 11, submerging sects. *Attenuata* and *Pistillata* in *Fimbriata* and *Pedatisecta,* respectively, and demoting sect. *Exappendiculata* to subsectional rank within sect. *Sinarisaema.*

Taking into account the rapidly fluctuating infrageneric taxonomy of *Arisaema,* the only subtaxa not represented in the present study are the monotypic subsect. *Exappendiculata* (H. Hara) J. Murata, and sects. *Decipientia* Engl. and (as far as can be determined) *Clavata.* Pollen of *A. exappendiculatum* and of *A. rhizomatum* (sect. *Decipientia*) is depicted in SEM micrographs of Murata (1984), and presents no peculiarities. Pollen of *A. heterocephalum* (sect. *Clavata*), pictured by Ohashi & Murata (1980) and Ohashi et al. (1983), has blunt spines, with the interspinal exine surface distinctly verruculate.

For all the controversy, this is one of the most palynologically uniform of the larger aroid genera, as abundantly illustrated in the study of Ohashi et al. (1983), and certainly the most well-studied.

According to Li (1979), *A. consanguineum* is a synonym of *A. erubescens* (Wallich) Schott, and *A. wallichianum* of *A. propinquum* Schott.

Specimens Examined: A. amurense Maxim.-P (P-3788), *Lee & Lee 109* (US), Korea. *A. candidissimum* W. Smith-Fr (PS-375), cult. M; (P-3789), *Rock 5053* (US), Yunnan. *A. concinnum* Schott-S (P-3790), *Nicolson 3367* (US), Nepal. *A. consanguineum* Schott-S (PS-6), *Deng & Yao 79029* (MASS), China. *A. dracontium* (L.) Schott-To (PS-7), *Allen 6877* (MASS), Louisiana. *A. fimbriatum* Masters-Fb (PS-281), *Burtt 1752* (E), cult. M. *A. flavum* Schott-D (PS-331), *Parker 3355* (A/GH), India. *A. franchetianum* Engl.-Fr (P-3791), *Rock 4658* (US), Yunnan. *A. jacquemontii* Blume-Tp (PS-185), *Mohindar Nath 56* (NY), India. *A. lichiangense* W. Smith-Fr (**P-3792**), *Rock 3391* (US), Yunnan. *A. macrospathum* Benth.-To (P-3787), *Hinton 4042* (US), Mexico. *A. murrayi* (J. Graham) Hook.-S (P-3793), *Saldanha 13656* (US), India. *A. nepenthoides* (Wallich) C. Martius-A (PS-183), *Kingdon Ward 446* (NY), Burma. *A. ringens* Schott-P (PS-178), *Wright s.n.* (NY), Harbor I. *A. serratum* (Thunb.) Schott-P (PS-272), *Bogner 1604* (M), Japan. *A. speciosum* (Wallich) C. Martius-Ts (PS-378), cult. M. *A. tortuosum* (Wallich) Schott-To (**P-3794**), *Nicolson 3336* (US), Nepal. *A. triphyllum* (L.) Schott-P (PS-9), *Boufford 14500* (MASS), North Carolina. *A. wallichianum* Hook. f.-Ts (PS-180), *Koelz 266* (NY), Himalayas. *A. yunnanense* Buchet-Fb (PS-330), *Ching 20761* (A/GH), Yunnan. *Section Annotations:* A = *Arisaema;* D = *Dochafa* (Schott) H. Hara; Fb = *Fimbriata* Engl.; Fr = *Franchetiana* Engl.; P = *Pedatisecta* Schott ex Engl.; S = *Sinarisaema* Nakai; To = *Tortuosa* Engl.; Tp = *Tenuipistillata* Engl.; Ts = *Trisecta* Schott.

Genus: **Ariopsis** Nimmo Figures 357, 358.

Taxonomic Reference: Engler & Krause, 1920.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *sym-*

metry radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small; mean 20 µm. EXINE SCULPTURING spinose, with short, sharp, broad-based spines; interspinal exine surface psilate, or very obscurely verruculate.

Specimen Examined: A. peltata Nimmo (**PS-235**), *Bogner 1481* (M), cult. M.

Genus: **Pinellia** Ten. Figures 359–361; 487.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: P. ternata (Gu & Hsu, 1991; Iwanami et al., 1988); *P. tripartita* (Uhlarz, 1985); *P. yaoluopingensis* (Gu & Hsu, 1991).

Species Examined: 3/8.

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE small to medium-sized; mean 25 µm, range 21 (*P. cordata*)–29 (*P. tripartita*) µm. EXINE SCULPTURING spinulose, with low, flattened, very broad-based yet sharply apiculate spinules that are closely approximate (or even abutting) on the surface of the grain. Interspinular surface ± verrucate and remotely punctate-foveolate (*P. angustata, P. ternata*), to moderately (*P. tripartita*) or conspicuously (*P. cordata*) foveolate, as in *Theriophonum*.

REMARKS: Hotta (1970) listed *P. angustata* in synonymy under *P. ternata*. Indeed, pollen from specimens identified by these names is indistinguishable in all respects.

Specimens Examined: P. angustata Schott (**P-3746**), *Bonati 3664B* (US), Yunnan. *P. cordata* N. E. Br. (**PS-97**), *Deng & Yao 79084* (MASS), China. *P. ternata* (Thunb.) Breitenb. (PS-121), *Madison 7572* (SEL). *P. tripartita* (Blume) Schott (PS-275), cult. M.

Genus: **Pseudodracontium** N. E. Br. Figures 362, 363; 432.

Taxonomic Reference: Serebryanyi, 1992.

Species Examined: 2/4.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 48 µm (*P. lacourii*); measurements of pollen of the remaining three species, calculated from SEM micrographs, are closely approximate. EXINE SCULPTURING narrowly striate, the striae rather narrower than the furrows and many of the striae with a medial groove, at least for part of their length. Striations in the "football" pattern (see "Remarks" under *Holochlamys*), all parallel from one end to the other. Grains auriculate, i.e., with ± prominent psilate lobes at either end.

REMARKS: This is a distinctive pollen type, and the species are superficially quite uniform. According to Serebryanyi (1992), *Pseudodracontium flotoi* equals *P. harmandii*, while *P. siamense* is a subspecies of *P. lacourii*.

Specimens Examined: P. flotoi S. Y. Hu (PS-321), *Floto 7738* (A/GH), Thailand. *P. harmandii* Engl. (PS-194), *Pierre s.n.* (NY), Vietnam. *P. lacourii* (Linden & André) N. E. Br. (PS-315), *Larsen et al. 856* (A/GH), Thailand; (PS-505), *Bogner 1663* (M), cult. M. *P. siamense* Gagnepain (**PS-413**), cult. K.

Genus: **Amorphophallus** Blume ex Decne. Figures 364–387; 434, 447, 463.

Taxonomic References: Engler, 1911; Stapf, 1923; Bogner, 1976, 1980e; Sivadasan, 1989.

Published SEM Micrographs: A. staudtii (Barthlott & Bogner, 1981; Knecht, 1983a); *A. abyssinicus, A. flavovirens* (Knecht, 1983a, b); *A. hildebrandtii* (Straka & Friedrich, 1984); *A. konjac* (Iwanami et al., 1988); *A. sumawongii* (Bogner, 1976; as *Thomsonia*); *A. asterostigmatus, A. hottae, A. palawanensis* (Bogner & Hetterscheid, 1992).

Species Examined: 23/120; *subgenera* 1/2; *sections* 5/10.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar to apolar. POLLEN SHAPE mostly boat-shaped-oblong to -elliptic (*A. bulbifer, A. eichleri*, plus all species with striate grains except *A. gallaensis*); occasionally spherical or subspheroidal, as in most nonstriate species (*A. prainii, A. lambii, A. titanum, A. paeoniifolius, A. abyssinicus, A. flavovirens, A. stuhlmannii, A. konjac* plus *A. gallaensis*); *symmetry* bilateral to radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE large; mean 53 µm, range 34 (*A. konjac*)–82 (*A. stuhlmannii*) µm. Pollen of *A. borneense* averages only 19 µm measured from SEM micrographs. Striate pollen (mean 46 µm, range 41 (*A. longituberosus*)–63 (*A. sutepensis*) µm, is on the average significantly smaller than nonstriate pollen (mean 61 µm, range 46 (*A. abyssinicus*)–82 µm), though there is considerable overlap. (*Amorphophallus konjac*, with pollen of an intermediate type, was not included in either category; if it were, the broad picture would not be altered.) EXINE SCULPTURING Approximately half the species examined have striate pollen. *Amorphophallus longituberosus* and *A. putii* (and, to a much lesser degree, *A. napalensis*) have striate-reticulate pollen—i.e., a reticulate pattern is evident between the striae; in *A. putii*, the striae are obscurely subfoveolate. The remaining striate species have psilate striae and furrows, the striae anastomosing sparingly and varying from narrow and many (*A. kerrii*) to broad and few (*A. gallaensis*). The basic pattern of striation for all striate species is the "football" type, with the striae converging to a point at each end; however, this breaks down into a swirling pattern on at least one lateral face of many grains in *A. kerrii, A. napalensis, A. sutepensis*, and *A. corrugatus*. In *A. variabilis*, the striae meet along a line rather than at a point. Some striae in *A. borneensis* and *A. sutepensis* bear a median groove, as in *Pseudodracontium*.

Nonstriate grains vary from almost perfectly psilate (*A. lambii, A. prainii, A. eichleri, A. bulbifer*) to sparingly punctate-foveolate (*A. titanum*) or -fossulate (*A. margaritifer*), or sparingly (*A. stuhlmannii*) to densely verrucate with large, hemispherical or oblong verrucae (*A. silvaticus, A. schweinfurthii, A. abyssinicus*), or spinose with long, stout, straight-sided spines (*A. flavovirens*). The interverrucal or interspinal exine surface is psilate, except in *A. schweinfurthii*, where it may be fossulate-verruculate.

The only two nonstriate species with decidedly boat-shaped pollen are *A. bulbifer* and *A. eichleri*, both with psilate exine. On pollen of the former species, a weak median keel is apparent on the presumably proximal face; this pollen is indistinguishable from that of many species of *Philodendron*, for example. *Amorphophallus bulbifer* is a sterile triploid ($2n = 39$) that reproduces mostly vegetatively. The pollen is overwhelmingly sterile as established via acetocarmine staining during the present investigations, yet fertile seeds are in fact produced (J. Bogner, pers. comm.).

Pollen of *A. konjac* appears intermediate between the striate and psilate conditions; the exine in this species is deeply and coarsely fossulate, with the surface broken up into large, flat, psilate plates.

REMARKS: *Amorphophallus* is the most diverse genus in Araceae palynologically (*Syngonium* being a close second). The whole range of diversity occurs within the huge sect. *Conophallus*, which spans nearly the entire geographic distribution of the genus. In view of this, it would be extremely interesting to know something of pollen morphology in the remaining nine sections of subg. *Amorphophallus* as well as in the monotypic subg. *Metandrium* Stapf. Material from these taxa proved most difficult to obtain, and the West African sections *Dracontiopsis* Engl. and *Corynophallus* (Schott) Engl., the Indochinese sect. *Interruptiflorus* Engl. and the East Asian sect. *Dysamorphophallus* Engl., in addition to subg. *Metandrium*, are unrepresented in this study. The available material of sects. *Amorphophallus* (*A. paeoniifolius*) and *Raphiophallus* (*A. margaritifer, A. silvaticus*) was only marginally acceptable.

Relatively few observations of taxonomic merit can be made within the genus. Striate grains appear nearly restricted to sect. *Conophallus*, having been observed elsewhere only in the oligotypic sect. *Rapyogkos* (*A. longituberosus*). The latter plus the remaining four investigated sections of *Amorphophallus* could be accommodated easily in sect. *Conophallus* from the palynological standpoint.

The two members of the African sect. *Hydrosme* investigated (*A. abyssinicus, A. schweinfurthii*) both have nonstriate (verrucate) pollen, but the same is true of most African members of sect. *Conophallus* (*A. flavovirens, A. eichleri, A. hildebrandtii, A. johnsonii, A. stuhlmannii, A. staudtii*); the only African species with striate pollen yet discovered is *A. gallaensis*, and it is somewhat aberrant in having nearly spherical grains with few, broad striae. Conversely, no Asian species with verrucate or spinose pollen are yet known in sect. *Conophallus* (all nonstriate species being psilate or nearly so). The only Asian species in the genus with verrucate pollen is *A. silvaticus* (sect. *Raphiophallus*).

Barthlott & Bogner (1981) depicted and described pollen of *A. staudtii* as psilate, Knecht (1983a, b) as foveolate—a condition virtually unknown in this genus. The latter author also portrayed pollen of *A. flavovirens* as striate; obviously, the same name is being employed for two different entities. She described (but did not illustrate) pollen of *A. johnsonii* as "scabrous."

The remarkable diversity of exine sculpturing in *Amorphophallus* sect. *Conophallus* does not necessarily imply that the section is unnatural (see Discussion); nearly comparable examples exist in other aroid genera (*Syngonium* sect. *Syngonium*) as well as in other families, e.g., in *Tournefortia* sect. *Tournefortia* (Boraginaceae) (Nowicke & Skvarla, 1974). *Amorphophallus* is in dire need of revision, and anyone undertaking such a task would be ill-advised to neglect pollen morphology.

Stout (1937) has reported that up to 80% of the pollen produced by *A. titanum* consists of small, sterile grains. In addition to that species, I observed this phenomenon in *A. prainii, A. lambii, A. kerrii*, and *A. putii*. Sterile grains of the last two species (the fertile pollen of which is striate) are psilate—as noted also for *Pistia* by Thanikaimoni (1969). This observation may be germane to the case of *Amorphophallus bulbifer* (see above). This large-scale production of sterile pollen may act to cohere fertile grains in long, vermiform masses and/or stick them onto insect pollinators, as Stout (1937) suggested, or perhaps it functions as a cheap pollinator reward (cf. Simpson & Neff, 1981).

Needless to say, *Amorphophallus* is more than sufficiently eurypalynous to accommodate the recently annexed genera *Plesmonium* (*A. margaritifer*) and *Thomsonia* (*A. napalensis, A. sumawongii*). Bogner et al. (1985) placed the erstwhile members of the latter genus among species presently residing in sect. *Conophallus*, while aligning *A. margaritifer* with species apparently belonging to sect. *Raphiophallus*, as recently expanded by Sivadasan (1989; i.e., to include Engler's sect. *Synantherias*).

Li (1979) listed *Amorphophallus kerrii* in synonymy under *A. yunnanensis* Engl.

Specimens Examined: A. abyssinicus (A. Rich.) N. E. Br.-H (P-3643), *Ash 3506* (US), Ethiopia. *A.* cf. *borneensis* (Engl.) Engl. & Gehrm.-Co (P-3639), *Ashton S21586* (US), Sarawak. *A. bulbifer* Blume-Co (**PS-278**), cult. M (acc. no. 22 80; orig. Nepal). *A. corrugatus* N. E. Br.-Co (**PS-126**), *Bogner 375* (M), Thailand. *A. eichleri* (Engl.) Hook. f.-Co (PS-266), *Bogner 591* (M), cult. M. *A. flavovirens* N. E. Br.-Co (**PS-270**), *Bogner 1591* (M), Senegal. *A. gallaensis* Engl.-Co (PS-517), *Greenway s.n.* (K), cult. K (acc. no. 326-56.32601; orig.

Kenya). *A. kerrii* N. E. Br.-Co (**PS-422**), cult. K (orig. Thailand). *A. konjac* K. Koch-Co (**PS-15**), *Moldenke 21949* (MASS), cult. New York. *A. lambii* Mayo & Widj.-Co (PS-232), *Lamb s.n.* (K), Sabah. *A. longituberosus* (Engl.) Engl. & Gehrm.-Rk (**P-3635**), *Bogner 371* (US), Thailand. *A. margaritifer* (Roxb.) Kunth-Rp (**PS-411**), *Griffith 6003* (K), E. Himalayas. *A. napalensis* (Wallich) Bogner & Mayo-Co (PS-456), *Koeltz 29477* (US), Assam [India]. *A. paeoniifolius* (Dennst.) Nicolson-A (P-3640), *A. C. Smith 6341* (US), Fiji. *A. prainii* Hook. f.-Cu (PS-518), cult. K. (acc. no. 472-82.04993; orig. Malaya). *A. putii* Gagnepain-Co (**PS-279**), *Bogner 429* (M), Thailand. *A. schweinfurthii* (Engl.) N. E. Br.-H (P-3644), *Dummer 2823* (US), Uganda. *A. silvaticus* (Roxb.) Kunth-Rp (P-3638), *Kunda & Balakrishnan 664* (US), Ceylon [Sri Lanka]. *A. stuhlmannii* (Engl.) Engl.-Co (PS-399), *Polhill & Wingfield 4623* (K), Tanzania. *A. sumawongii* (Bogner) Bogner & Mayo-Co (**P-3551**), *Bogner 368* (US), Thailand. *A. sutepensis* Gagnepain-I (PS-493), cult. K (acc. no. 473-82.05076; orig. Thailand). *A. titanum* Becc.-Co (**PS-99**), cult. M (acc. no. 3560/80; orig. Sumatra). *A. variabilis* Blume-Co (P-3641), *Nicolson 961* (US), cult. BO. *Section Annotations:* A = *Amorphophallus*; Co = *Conophallus* Schott emend. Engl.; Cu = *Cundaropsis* Engl.; H = *Hydrosme* (Schott) Engl.; I = sect. indet.; Rk = *Rapyogkos* Engl.; Rp = *Raphiophallus* (Schott) Engl. (All subg. = *Amorphophallus*.)

Genus: **Protarum** Engl. Figures 388–391; 464.

Taxonomic Reference: Engler, 1920.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean *21 μm, range *20–*22 μm. EXINE SCULPTURING striate, the striae psilate, fairly narrow, sparingly anastomosing, and in the "baseball" pattern of *Holochlamys* and *Steudnera*.

REMARKS: Sample PS-449 yielded apparently immature pollen but is depicted to show the pattern of the striae since numerous grains were photographed. Pollen from sample PS-412 is considered to exhibit more or less mature exine sculpturing, although exceedingly few grains were recovered.

Specimens Examined: P. sechellarum Engl. (**PS-412**), *Thomasset s.n.* (K), Seychelles; (**PS-449**), *Schimper s.n.* (B), Seychelles.

Genus: **Arisarum** Hill Figures 392, 393; 465.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: A. vulgare (Grayum, 1986c).

Species Examined: 1/3.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-elongate; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 45 μm, range 43–46 μm. EXINE SCULPTURING striate-foveoreticulate, the reticulum covering all surfaces of the grain. The striae run parallel, in the "football" pattern, but do not quite reach the ends. This is the only genus in Araceae with striate pollen in which the upper surfaces of the striae bear a reticulate pattern (but see *Amorphophallus putii*).

REMARKS: *A. simorrhinum* is generally merged with *A. vulgare*, or sometimes given varietal rank (e.g., Engler, 1920). Palynologically they are essentially identical.

Specimens Examined: A. simorrhinum DC. (P-3744), *Sennen 7811* (US), Spain. *A. vulgare* Targ.-Tozz. (**PS-10**), *Penchinat 2555* (MASS), France.

Genus: **Ambrosina** Bassi Figures 394, 395; 466.

Taxonomic Reference: Engler, 1920.

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE boat-shaped-oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 44 μm. EXINE SCULPTURING striate-reticulate, with narrow, undulate striae arranged in a parallel "football" pattern; striae breaking up into a verrucate pattern at either end of the grain. The reticulum occupies the bottom and walls of the furrows and is ± regularly segmented by vertical ribs (rugulae); the top surfaces of the striae are perfectly psilate.

REMARKS: See "Remarks" under *Pistia*.

Specimen Examined: A. bassii L. (**PS-118**), *Bogner 1521* (M), Sardinia.

Genus: **Pistia** L. Figures 396, 397; 433, 467.

Taxonomic Reference: Engler, 1920.

Published SEM Micrographs: P. stratiotes (Kuprianova & Tarasevich, 1984; Bogner, 1987).

Species Examined: 1/1.

POLLEN TYPE: *aperture type* inaperturate; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elongate to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 27 μm. EXINE SCULPTURING plicate, with thin, high, strongly undulate frills running the length of the grains in a "football" pattern. All surfaces virtually psilate, except that the frills bear low vertical "ribs" (rugulae) that are briefly decurrent onto the furrows.

REMARKS: There appears to be no basis at the light microscope or SEM level for Thanikaimoni's (1969) contention that pollen of *Pistia* is monosulcate. No doubt the pollen tube exits in a tear between two plicae, as in *Spathiphyllum* (Erdtman, 1952); however, I can detect no evidence of a differentiated aperture. TEM studies will be required to settle the matter.

There are obvious, striking resemblances between pollen of *Pistia* and of *Ambrosina*. *Pistia* pollen has thinner, higher, more strongly undulate plicae, and has lost the reticulum, but it retains vestiges of the distinctive ribbed appearance. In contrast, the ulcerate, spherical, spinose pollen of the Lemnaceae, with which *Pistia* is traditionally aligned, appears very different.

Specimen Examined: P. stratiotes L. (**PS-98**), *Grayum 3079* (MASS), cult. MASS.

Discussion: The Evolution of Major Palynological Characters in the Araceae

The evolution of pollen characters in angiosperms has not been a major concern of palynologists until relatively recently. Most of the major palynological works of the present century (Wodehouse, 1935; Erdtman, 1952, 1969; Faegri & Iversen, 1964) are concerned mainly with matters of description, definition, and technique. Speculation regarding trends of character evolution lay widely scattered in pollen monographs and paleobotanical papers, and not until fairly recently, with the publication of papers by Muller (1970), Doyle (1973), Walker & Doyle (1975), Walker (1976), and Zavada (1983), has a consensus begun to emerge.

For Araceae, pollen character evolution is essentially unexplored, although isolated statements are scattered through the literature. Erdtman (1952) limited himself to a sentence or two, and Thanikaimoni (1969), author of the definitive light-microscopic survey of aroid pollen, ventured no opinion on the subject. This gap is filled by the following analysis of the data presented in the previous section.

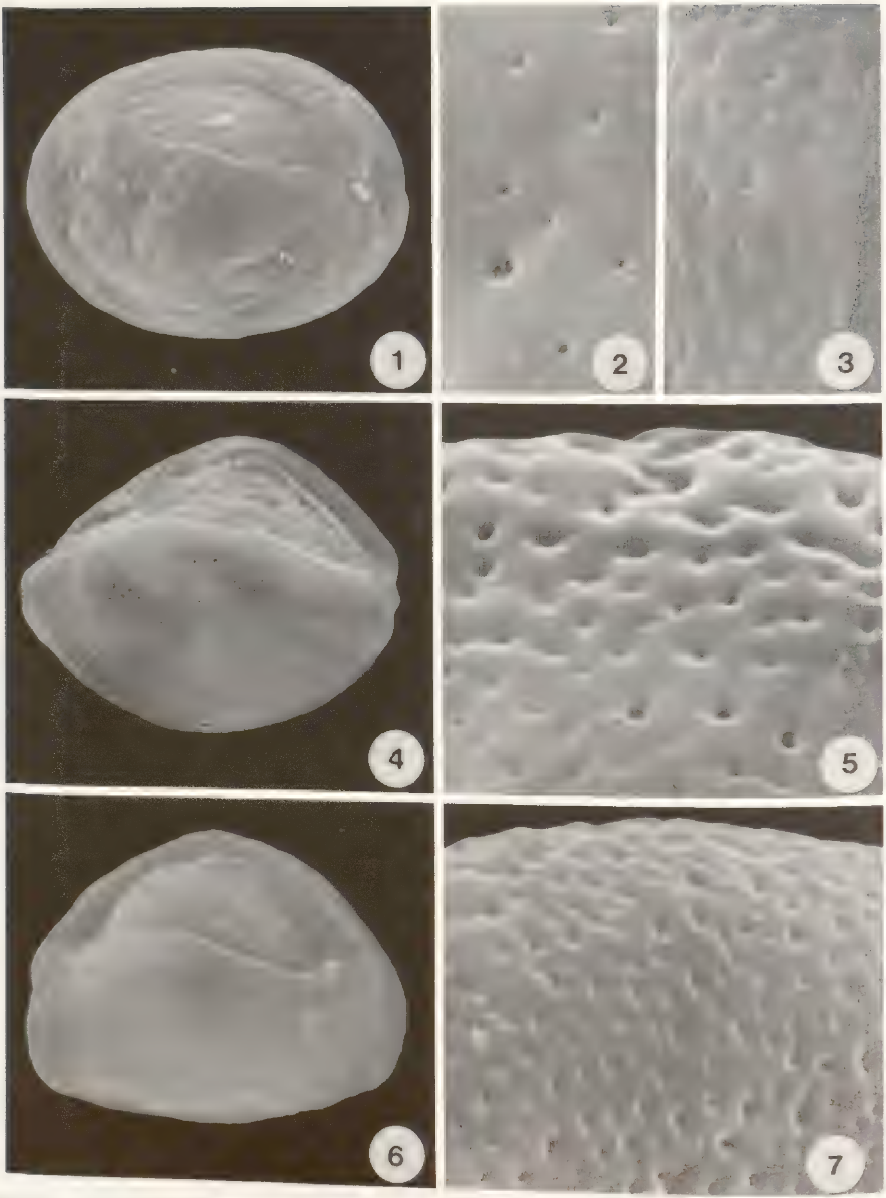
The major pollen characters are considered for Araceae in the following paragraphs in order of appearance in the standard generic pollen description format. The descriptive terminology employed is that of Erdtman and others as modified by Walker & Doyle (1975). For the sake of convenience, data for all genera on aperture type, pollen shape, mean pollen size, and exine sculpturing are presented in abbreviated form in Table 1. In addition, variation and taxonomic distribution of character-states of aperture type and exine sculpturing have been summarized pictorially for Araceae in Figures 398–488. Note that in the text that follows, major infrafamilial taxa referred to are those of the neo-Englerian system (see Bogner, 1978), incorporating nomenclatural changes indicated by Nicolson (1984).

APERTURE TYPE

Pollen of Araceae may be either aperturate or inaperturate. Of these two most basic types, inaperturate pollen (Figs. 414–435) is by far the most common, occurring in 77 of the 105 genera (or about 73%) for which information is available. This contrasts strikingly with the situation in such putative aroid relatives as palms (Thanikaimoni, 1970) and Cyclanthaceae (Harling, 1958), where inaperturate pollen is totally unknown. Only one of the eight aroid subfamilies, Calloideae (Figs. 124–136), lacks inaperturate pollen. Inaperturate and clearly aperturate pollen occur together in just three genera: *Anthurium* (Figs. 24–29), *Stenospermation* (Figs. 407, 417), and *Rhodospatha* (Figs. 119, 121) (cf. also the marginal cases in *Stylochaeton*, *Gearum* and *Gorgonidium*).

Aroid pollen features four major types of apertures: monosulcate, zonate, diaperturate, and forate. The first two account for the majority of aperturate genera; the others are less important. Monosulcate pollen, with a single, elongate furrow-like aperture (Figs. 398–402), is known from 17 genera (only about 16% of all aroid genera but about 63% of the genera with aperturate pollen); it occurs in *Acorus* and *Gymnostachys*, and throughout the tribes Potheae, Orontieae, and Lasieae. Zonate pollen, in which the aperture encircles the grain in a ringlike fashion (Figs. 404–408), is known in 10 genera (10% of all aroid genera, about 36% of aperturate genera), occurring in some species of *Heteropsis* and throughout the tribes Zamioculcadeae and Monstereae. Diaperturate pollen, i.e., with two separate apertures (Figs. 410–412), is now known from *Heteropsis*, *Rhaphidophora*, and *Calla*. Forate pollen, with several, scattered, porelike apertures (Fig. 413), is unique to *Anthurium*. Two additional subtypes of very limited occurrence, extended monosulcate and monosulcoidate, may also be distinguished; these are considered trivial and transitional forms.

There can be little doubt that aperturate pollen, notwithstanding its minority status in Araceae, represents the primitive condition, and that monosulcate pollen is the most primitive of the various aperturate types. These conclusions arise not only from in-group and out-group analysis, but from the comparatively rich angiosperm pollen fossil record.



FIGURES[3] 1–7. Pollen of *Acorus* [Acoraceae] (1–3), *Gymnostachys* (4, 5) and *Pothos* pro parte (6, 7). 1, 2, *A. calamus* (PS-1). Fig. 1, ×3,110. 3. *A. gramineus* (PS-2). 4, 5. *G. anceps* (P-3293). Fig. 4, ×2,470. 6, 7. *P. scandens* (P-3294). Figure 6, ×4,620.

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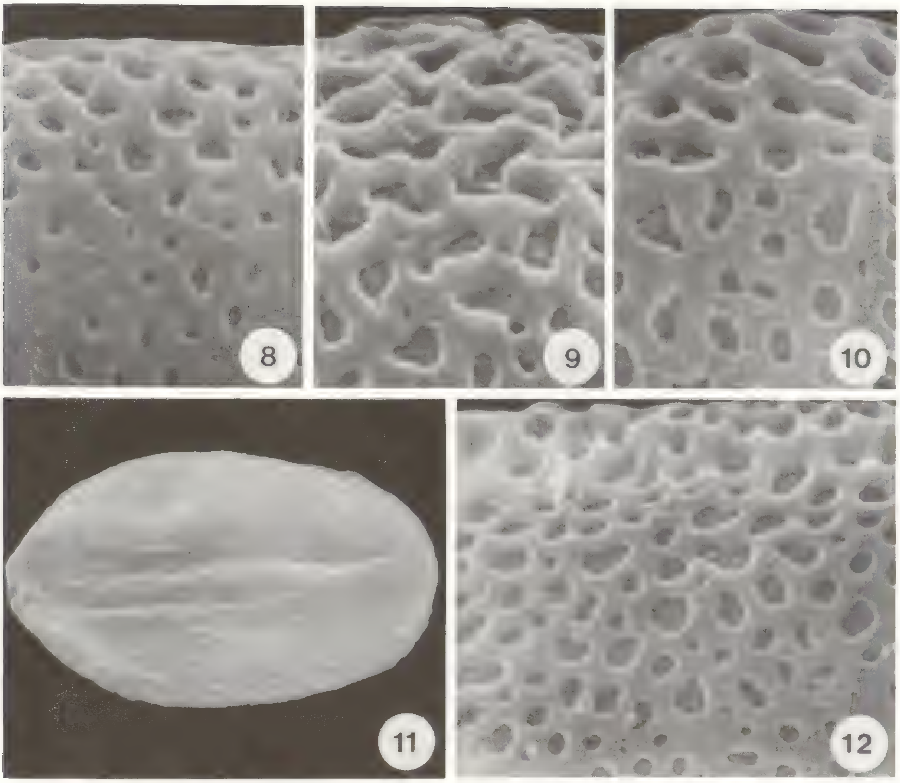
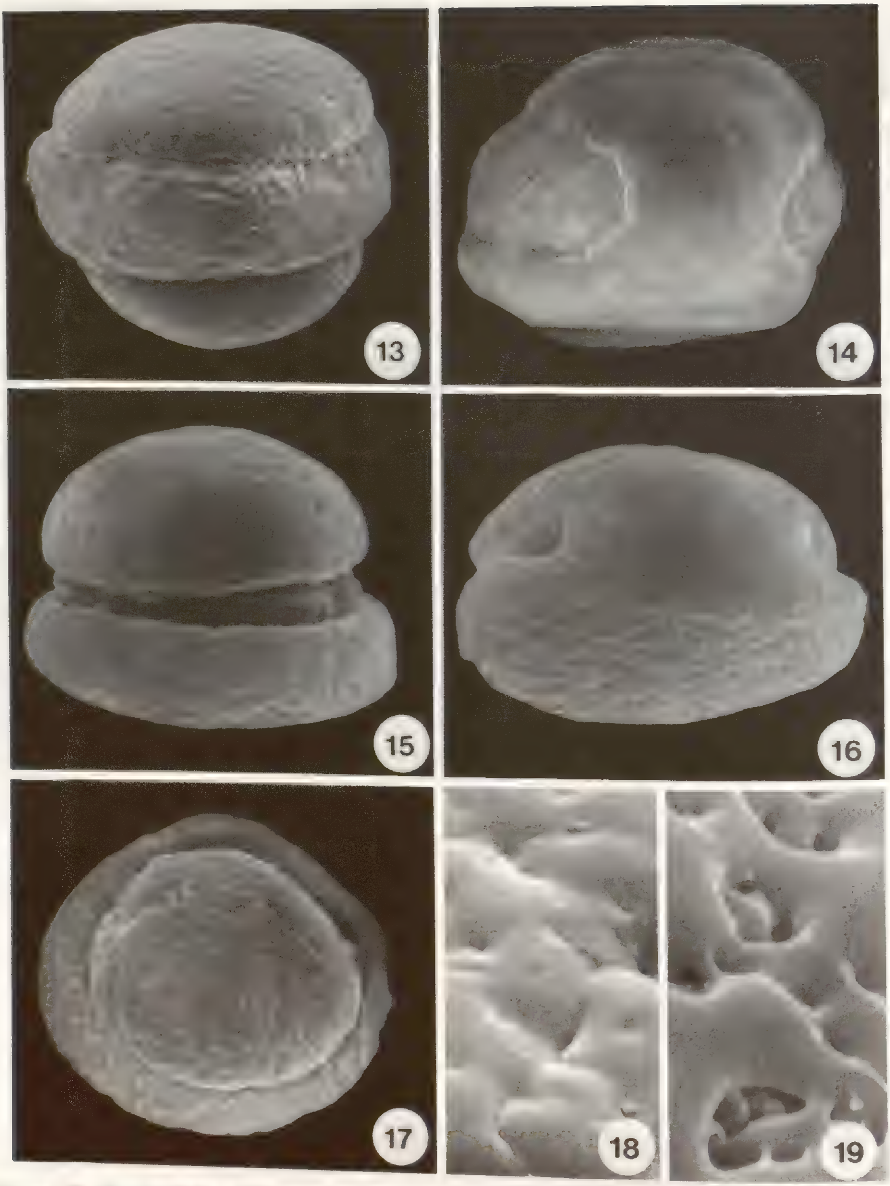
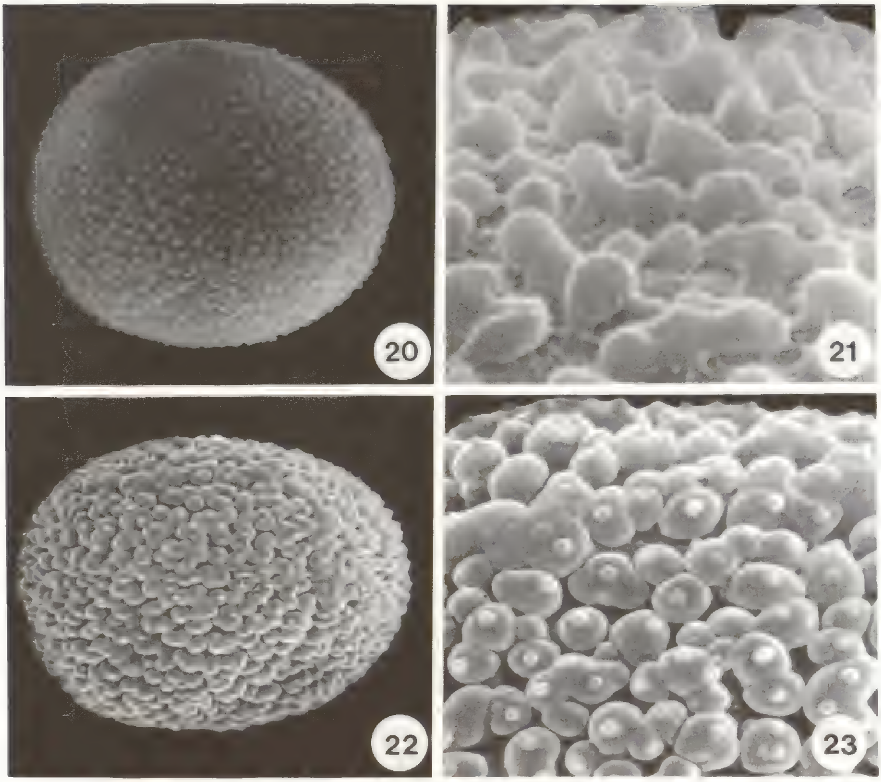
[3] Note for all figures: Magnifications are generally provided only for low-magnification (whole-grain) photographs. High-magnification (detail) photographs are all ×12,000, unless otherwise indicated.



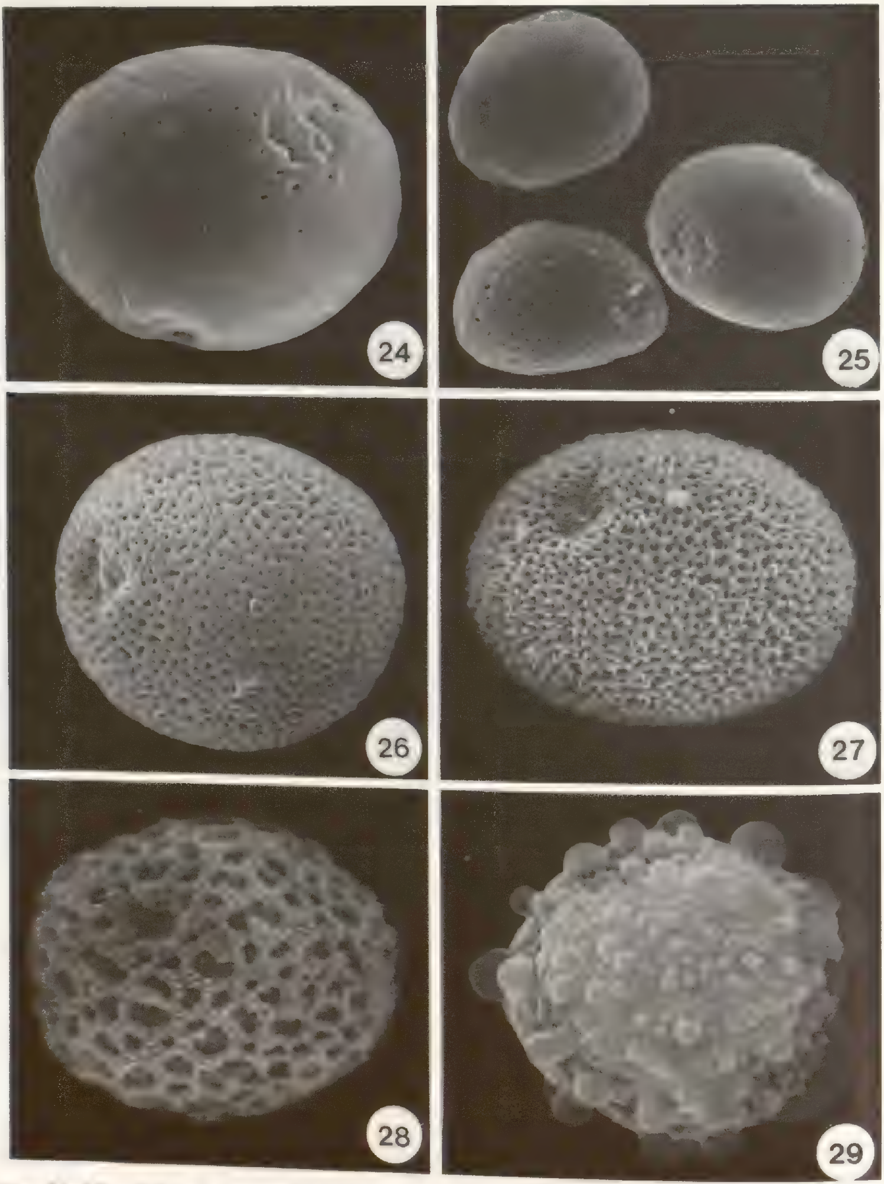
FIGURES 8–12. Pollen of *Pothos* pro parte (8–10) and *Pothoidium* (11, 12) (tribe Potheae). 8. *Pothos repens* (P-3296). 9. *Pothos remotiflorus* (P-3576). 10. *Pothos beccarianus* (PS-433). 11, 12. *Pothoidium lobbianum* (P-3536). Fig. 11, ×4,745.



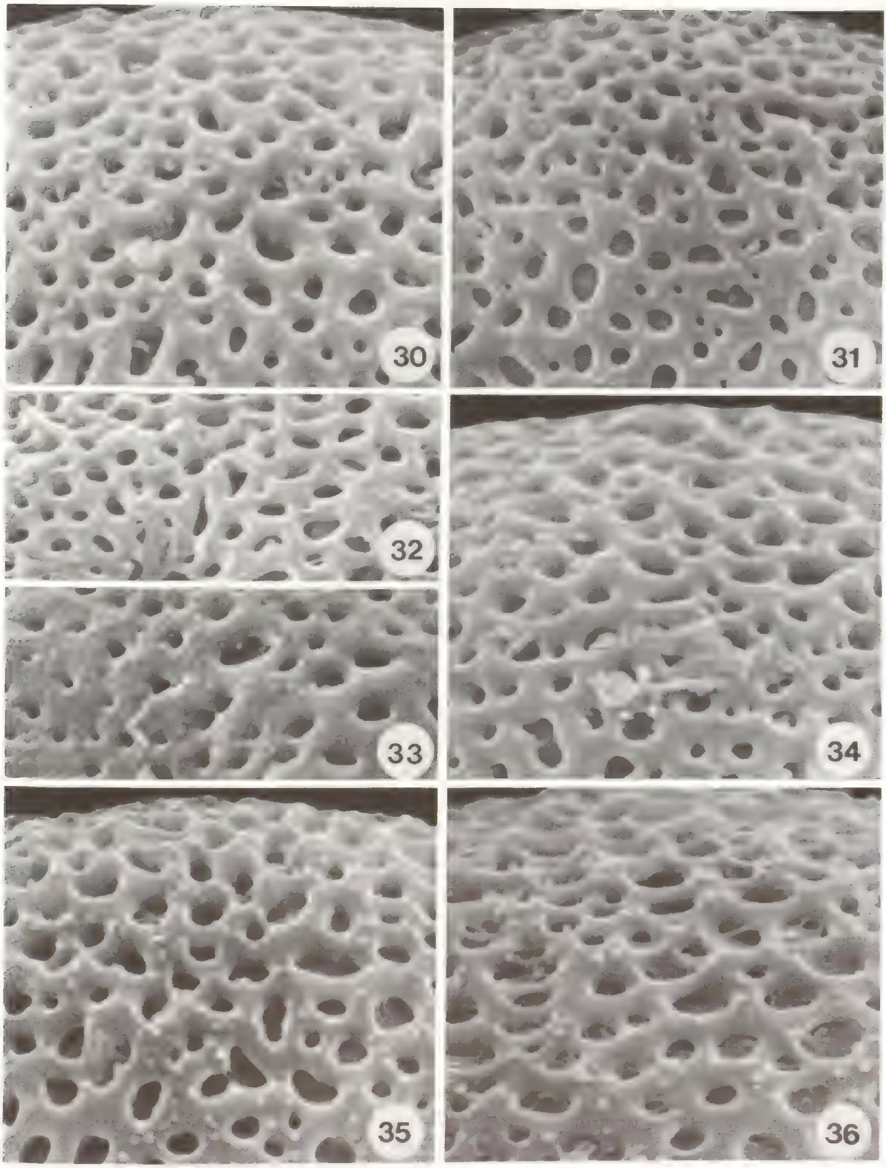
FIGURES 13–19. Pollen of *Zamioculcas* (13, 14, 18) and *Gonatopus* (15–17, 19) (tribe Zamioculcadeae). 13, 14, 18. *Z. zamiifolia* (PS-151). Fig. 13, ×1,000; Fig. 14, ×950. 15–17, 19. *G. angustus* (PS-274). Fig. 15, ×930; Fig. 16, ×920; Fig. 17, ×940.



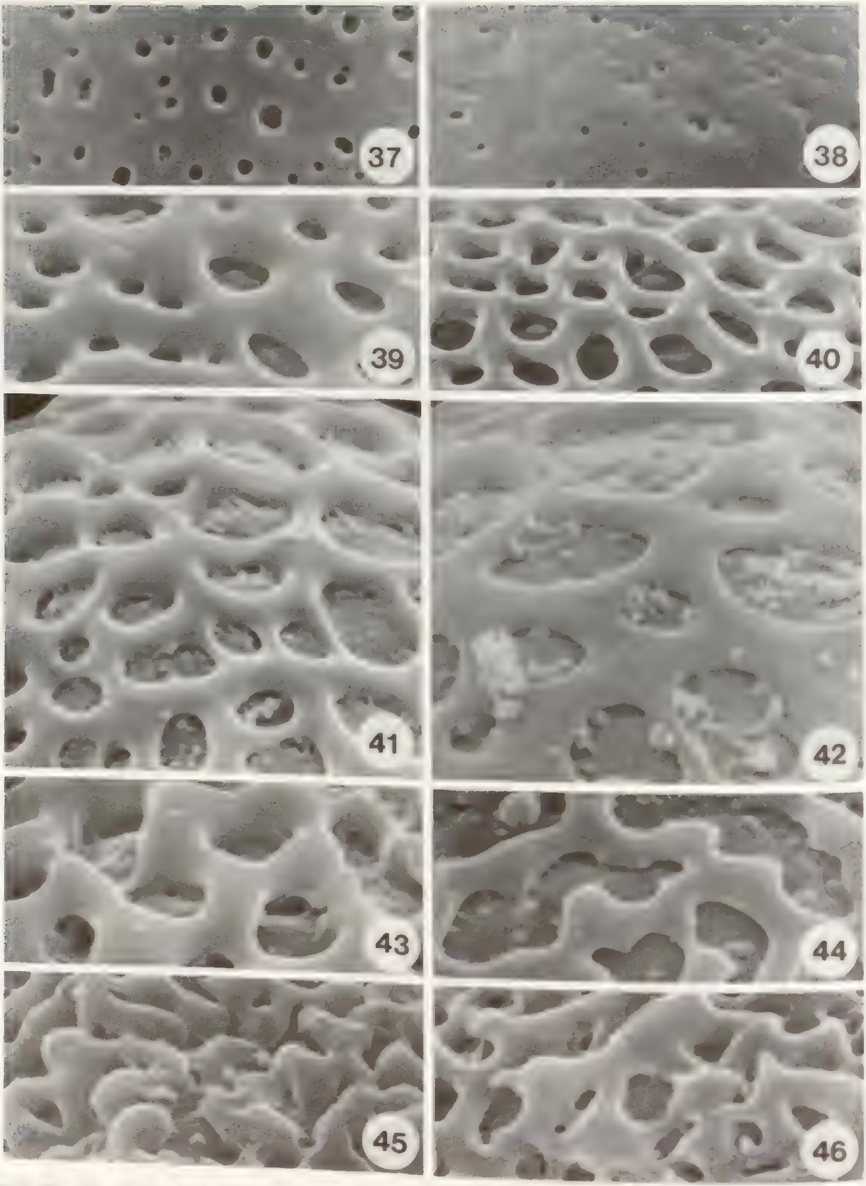
FIGURES 20–23. Pollen of *Culcasia* (20, 21) and *Anadendrum* (22, 23). 20, 21. *C. longevaginata* (PS-238). Fig. 20, ×1,415. 22, 23. *A. montanum* (PS-176). Fig. 22, ×3,695.



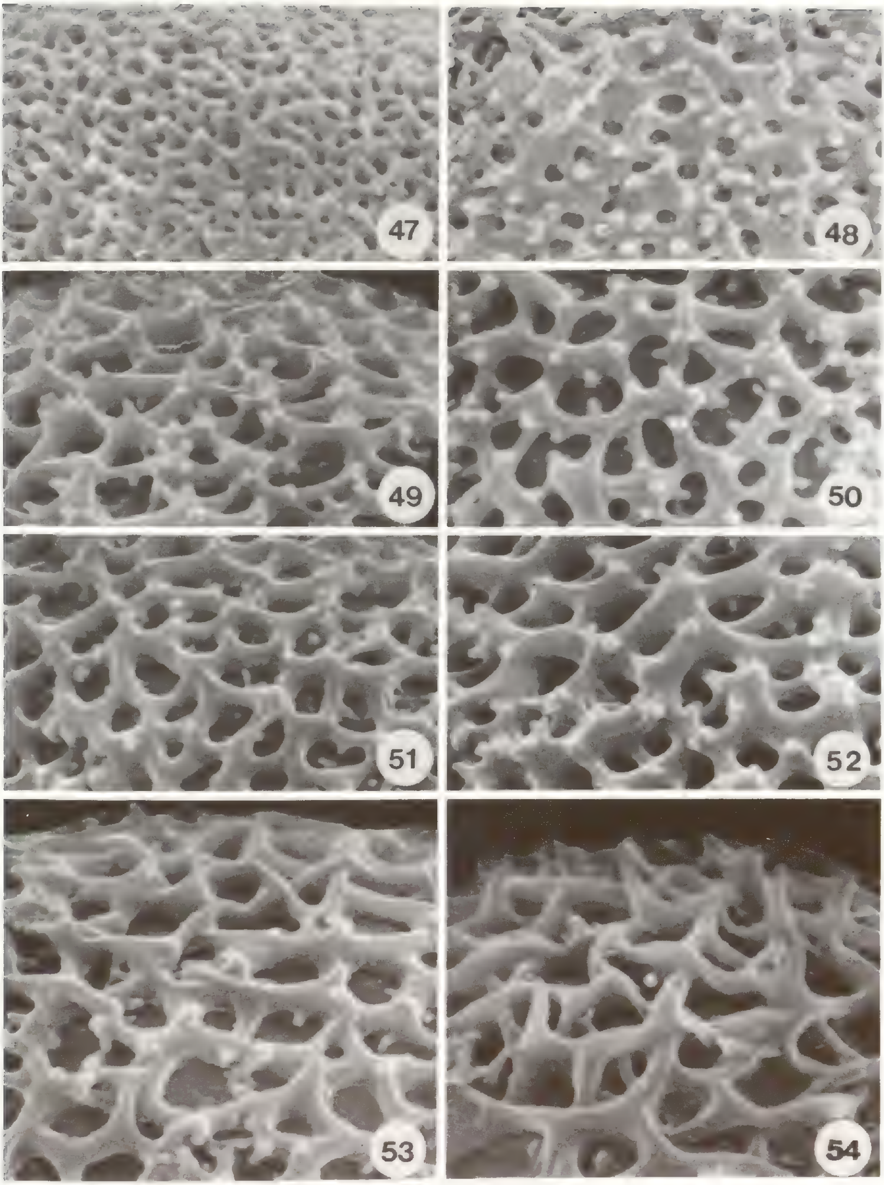
FIGURES 24–29. Pollen of *Anthurium* (whole grains). 24, 25. *A. pallidiflorum* (PS-156). Fig. 24, ×4,220; Fig. 25, ×2,650. 26. *A. protensum* (P-3765). ×3,510. 27. *A. subcoerulescens* (P-3761). ×3,005. 28. *A. redolens* (PS-224). ×3,380. 29. *A. clidemioides* (PS-109). ×3,410.



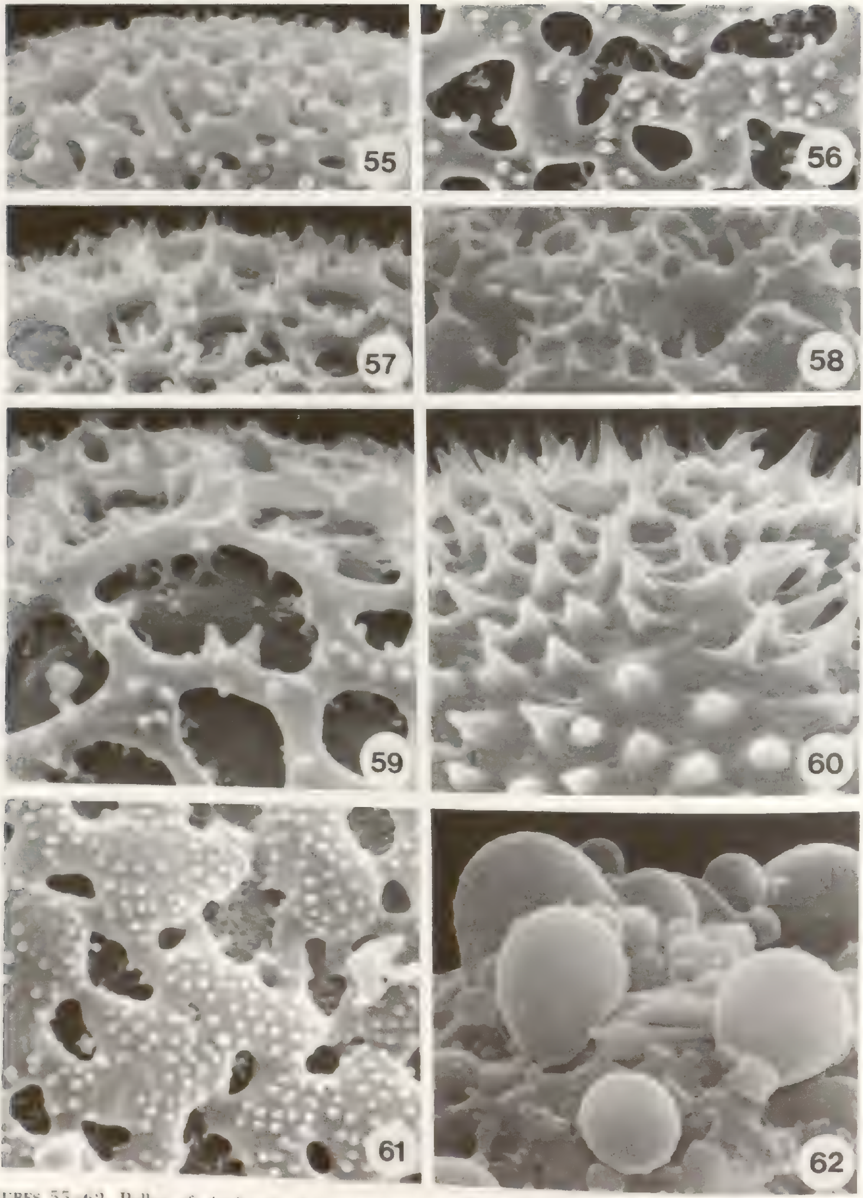
FIGURES 30–36. Pollen of *Anthurium* (exine surfaces; species with spinulose or scabrous muri). 30. *A. protensum* (P-3765). 31. *A. leucostachyum* (P-3768). 32. *A. dominicense* (PS-5). 33. *A. gymnopus* (P-3764). 34. *A. consobrinum* (P-3766). 35. *A. pedatum* (P-3772). 36. *A. validifolium* (PS-227).



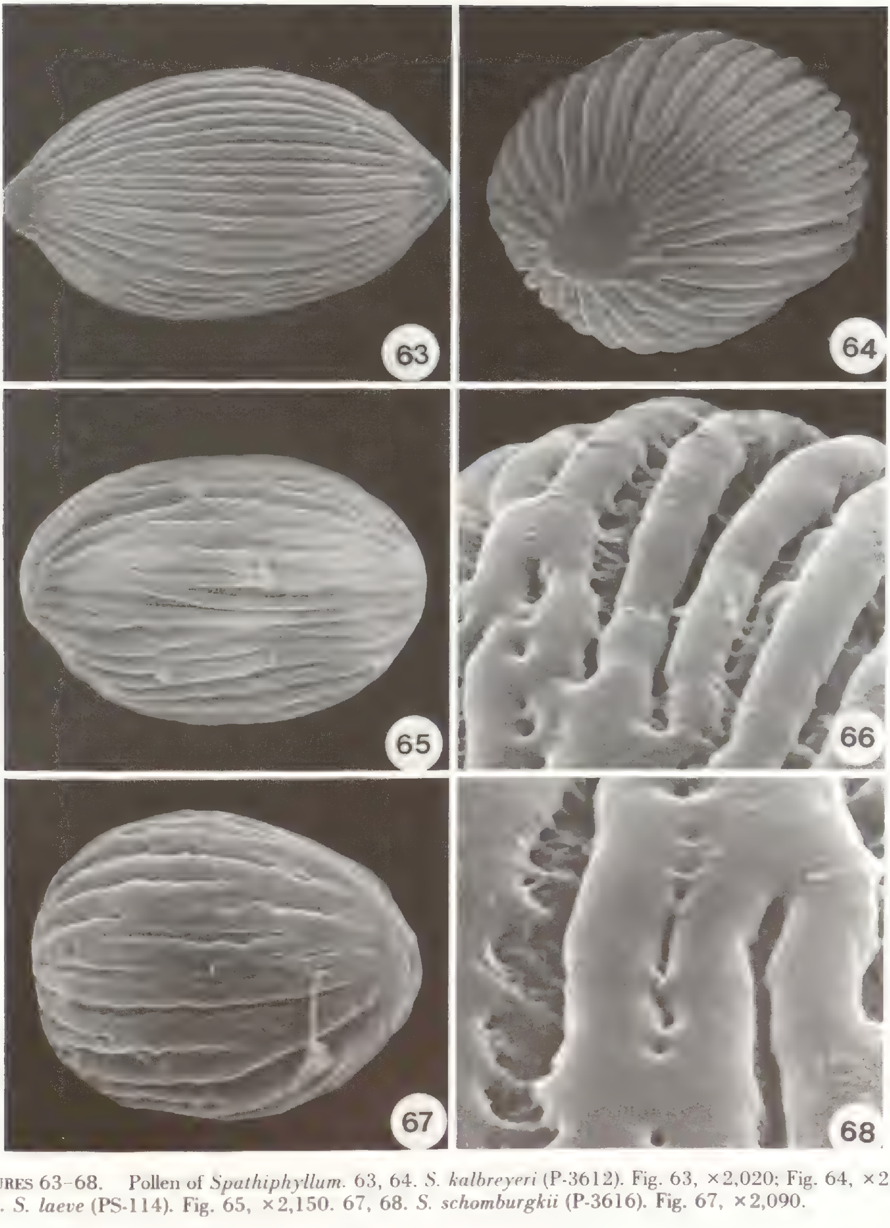
FIGURES 37–46. Pollen of *Anthurium* (exine surfaces; species with psilate muri). 37, 38. *A. pallidiflorum* (PS-156); different portions of the surface of a single grain (cf. Figs. 24, 25). 39. *A. tilaranense* (P-3771). 40. *A. pittieri* (P-3756). 41. *A. ovandense* (PS-220). 42. *A. magnificum* (PS-276). 43. *A. radicans* (PS-206). 44. *A. salvadorense* (PS-225). 45. *A. ovatifolium* (P-3773). 46. *A. polyschistum* (P-3582).



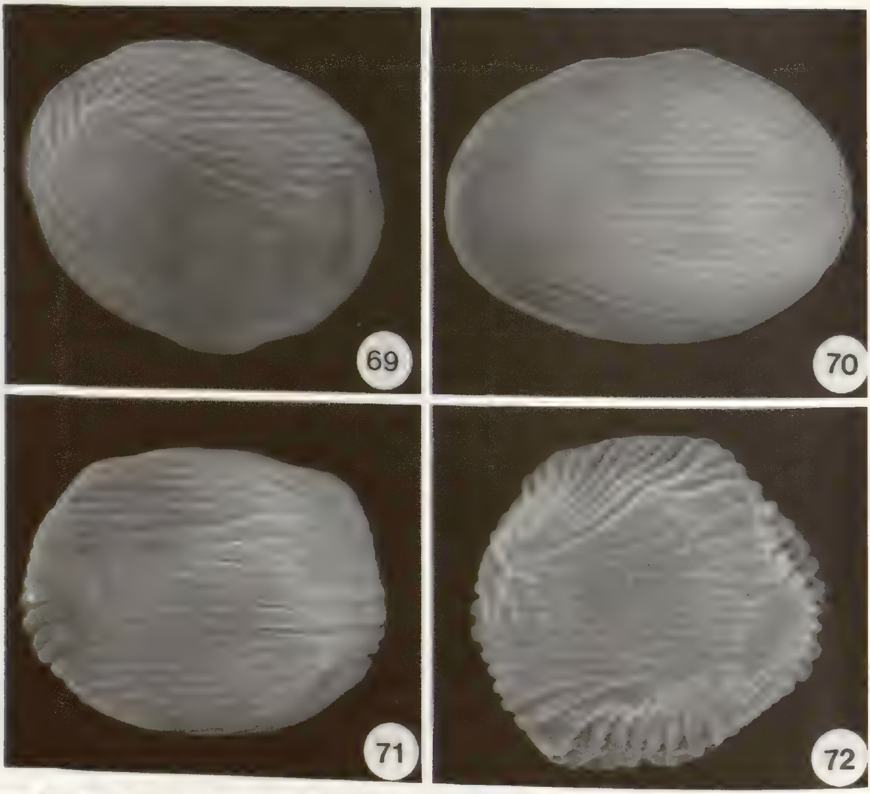
Figures 47–54. Pollen of *Anthurium* (exine surfaces; species with "criss-crossing" muri). 47. *A. lancea* (P-3769). 48. *A. rivulare* (P-3759). 49. *A. subcoerulescens* (P-3761). 50. *A. harrisii* (PS-215). 51. *A. lucens* (PS-217). 52. *A. reticulatum* (P-3760). 53. *A. longipeltatum* (PS-216). 54. *A. scherzerianum* (P-3752).



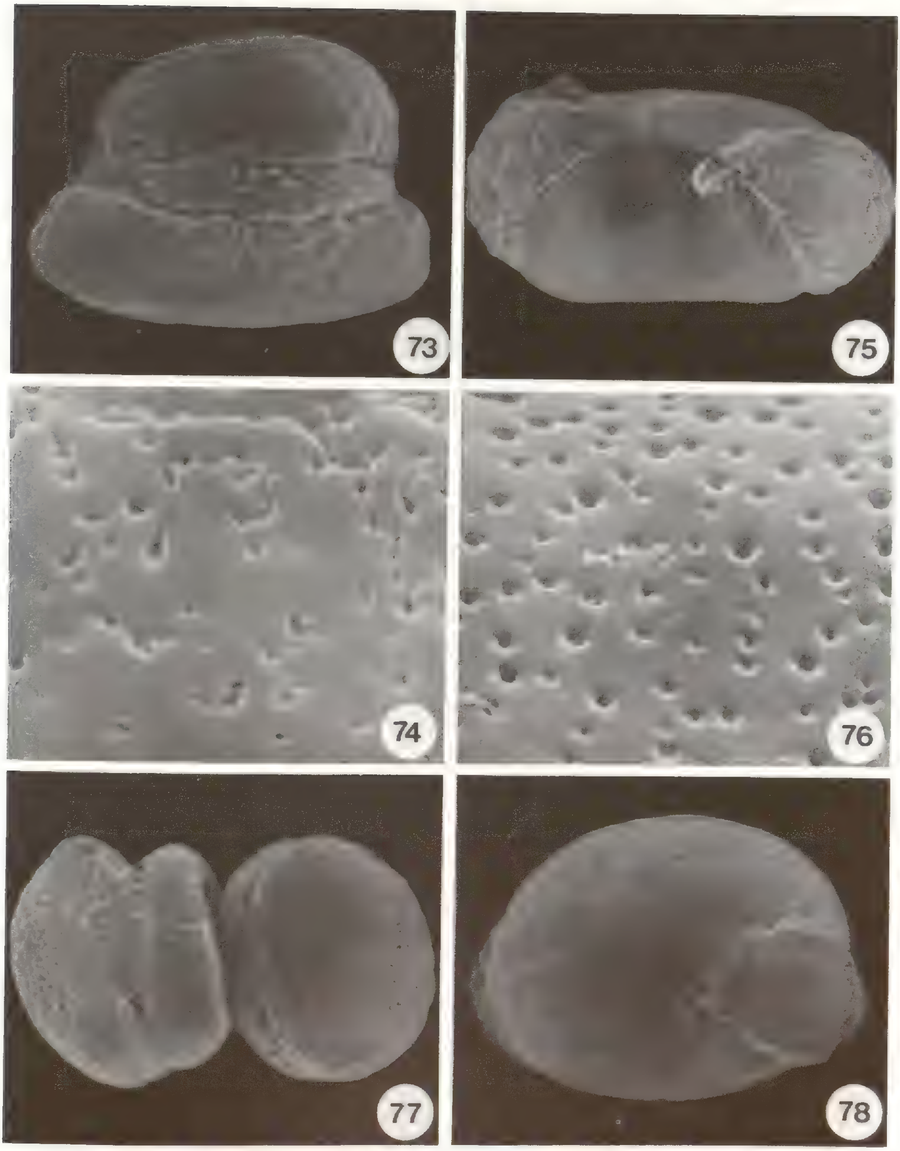
FIGURES 55–62. Pollen of *Anthurium* (exine surfaces; species with miscellaneous or unusual exine sculpturing). 55. *A. willdenowii* (PS-158). 56. *A. bellum* (PS-153). 57. *A. gracile* (PS-155). 58. *A. scandens* var. *leucocarpum* (PS-148). 59. *A. redolens* (PS-224). 60. *A. friedrichsthalii* (P-3755). 61. *A. amazonicum* (P-3767). 62. *A. clidemioides* (PS-109).



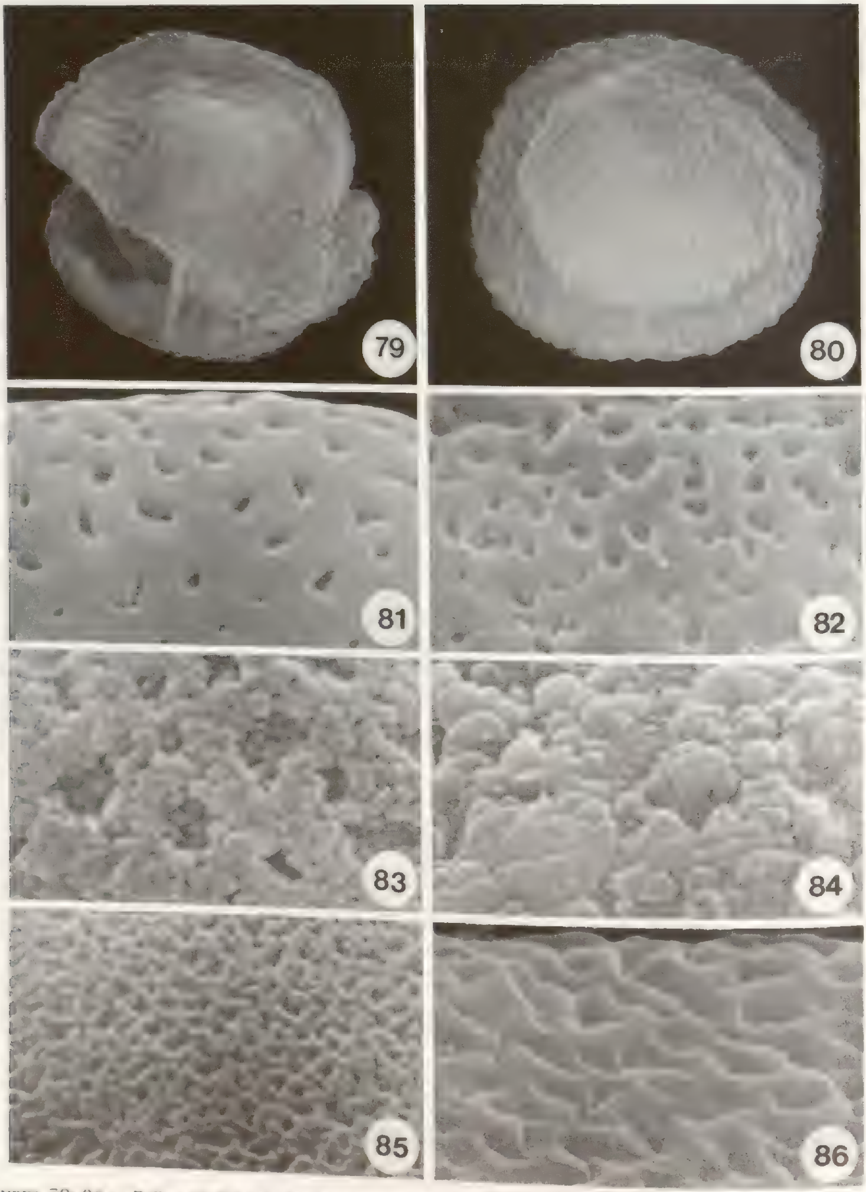
FIGURES 63–68. Pollen of *Spathiphyllum*. 63, 64. *S. kalbreyeri* (P-3612). Fig. 63, ×2,020; Fig. 64, ×2,600. 65, 66. *S. laeve* (PS-114). Fig. 65, ×2,150. 67, 68. *S. schomburgkii* (P-3616). Fig. 67, ×2,090.



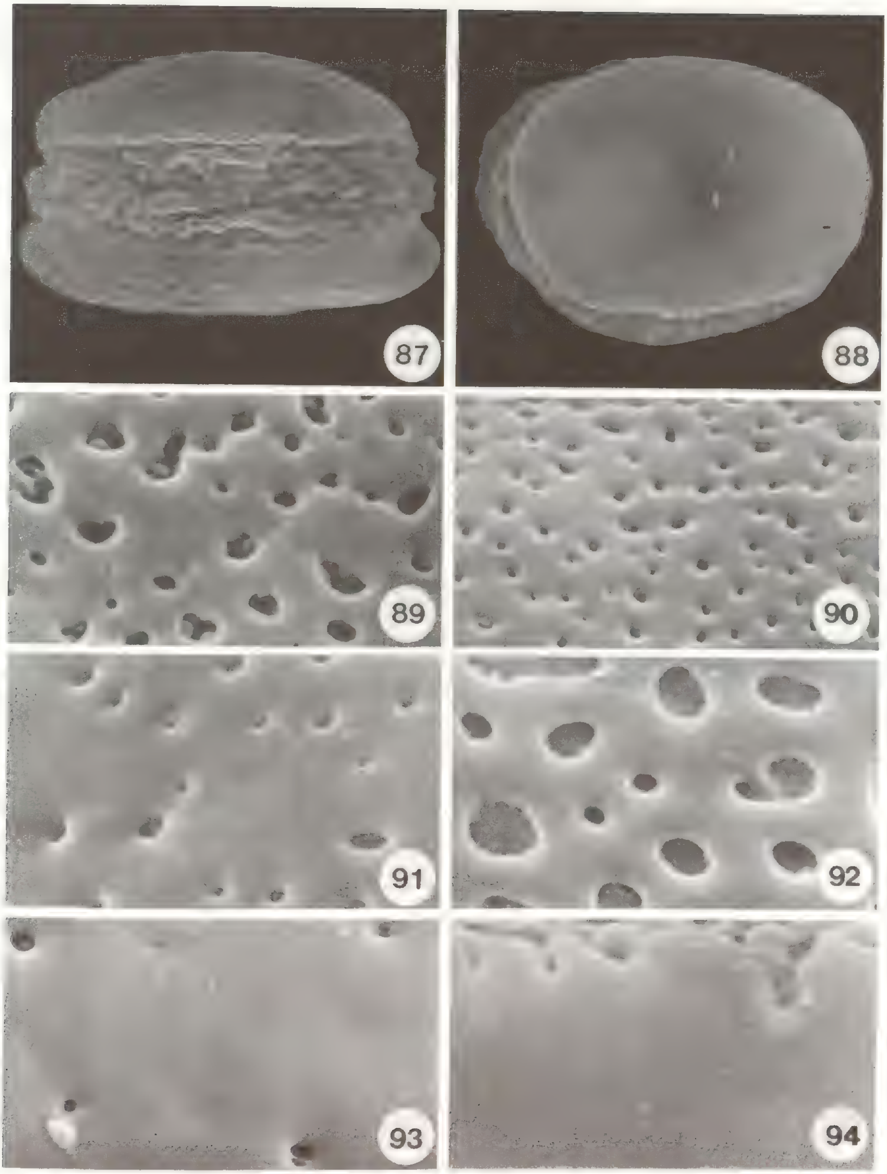
FIGURES 69–72. Pollen of *Holochlamys*. 69–72. *H. guineensis* (P-3548), as seen from different orientations. Fig. 69 (×2,770) is an oblique view showing portions of the following three orientations. Fig. 70 (×2,680) and Fig. 71 (×2,590) are "side" views showing the "converging" and "parallel" sides, respectively, and Fig. 72 (×2,540) is an "end" view of the nonconverging end (see pollen description of *Holochlamys* for further explanation).



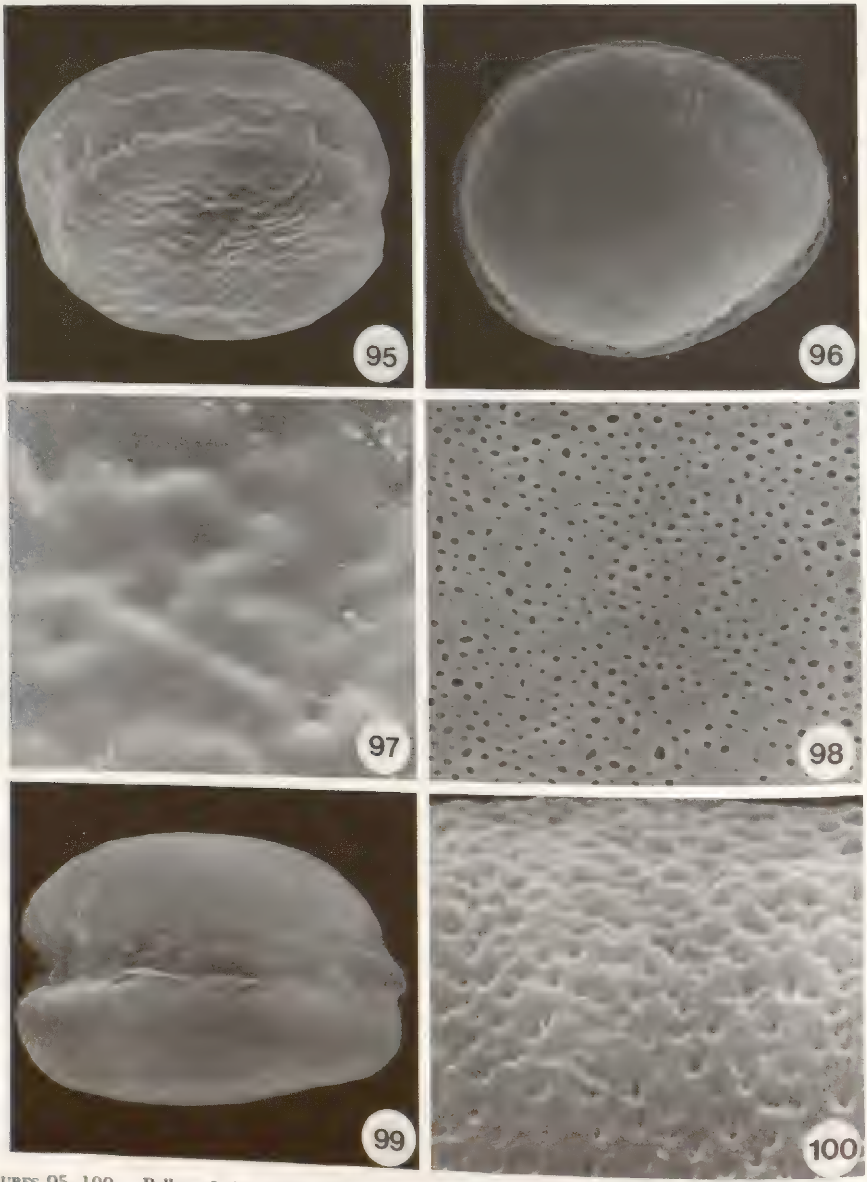
FIGURES 73–78. Pollen of *Heteropsis* (73–76) and *Rhaphidophora* pro parte (77, 78). 73, 74. *H. oblongifolia* (PS-359). Fig. 73, ×1,770. 75, 76. *H. integerrima* (PS-192). Fig. 75, ×1,330. 77. *R. africana* (PS-289). ×1,980. 78. *R. peeploides* (P-3544). ×2,780.



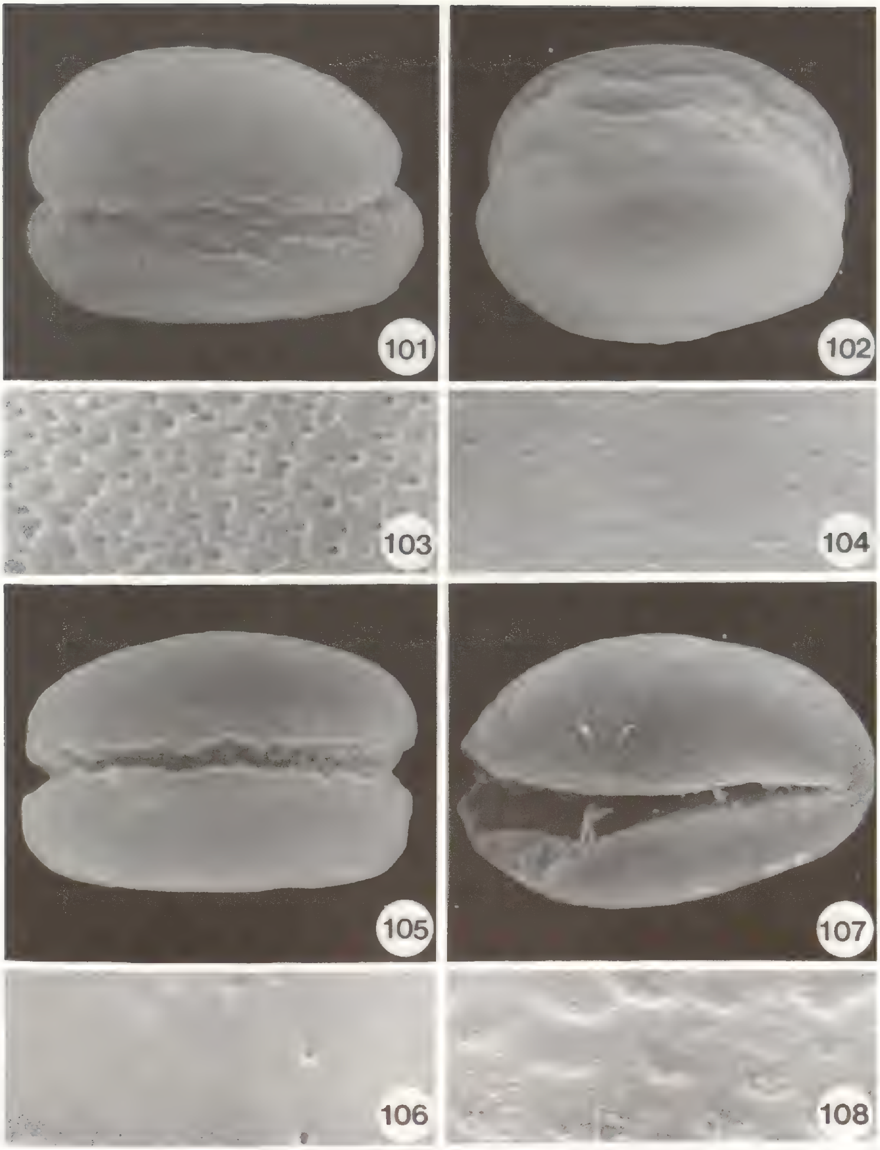
FIGURES 79–86. Pollen of *Rhaphidophora* pro parte. 79, 80, 84. *R. reineckei* (P-3595). Fig. 79, ×2,880; Fig. 80, ×2,610. 81. *R. montana* (P-3594). 82. *R. peeploides* (P-3544). 83. *R. africana* (PS-289). 85. *R. pertusa* (P-3591). 86. *R. graeffei* (P-3592).



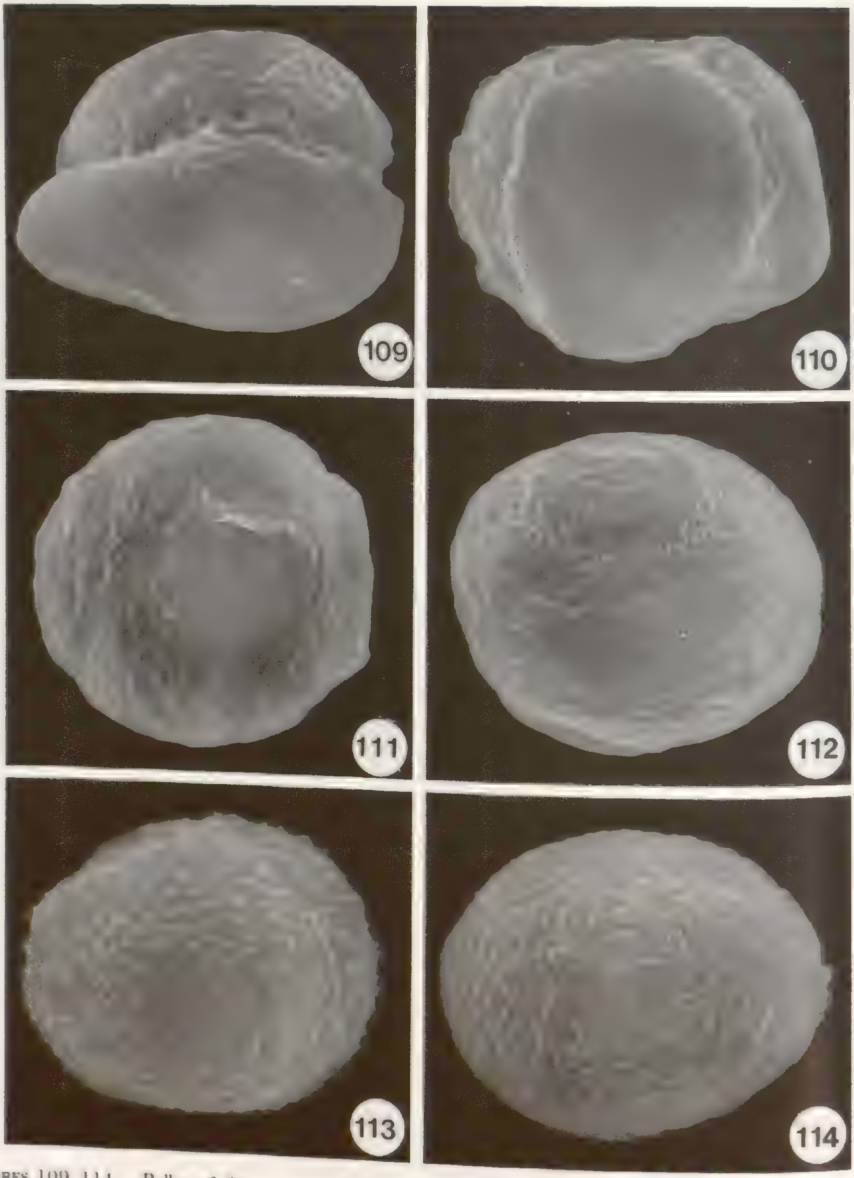
FIGURES 87–94. Pollen of *Monstera*. 87. *M. diversifolia* (PS-386). ×1,790. 88, 90. *M. skutchii* (P-3601). Fig. 88, ×1,260. 89. *M. tenuis* (P-3602). 91. *M. lechleriana* (P-3604). 92. *M. adansonii* var. *laniata* (P-3598); showing largest reticulum furthest from aperture. 93. *M. deliciosa* (PS-18). 94. *M. tuberculata* var. *brevinodum* (PS-340); portion of exine near the aperture.



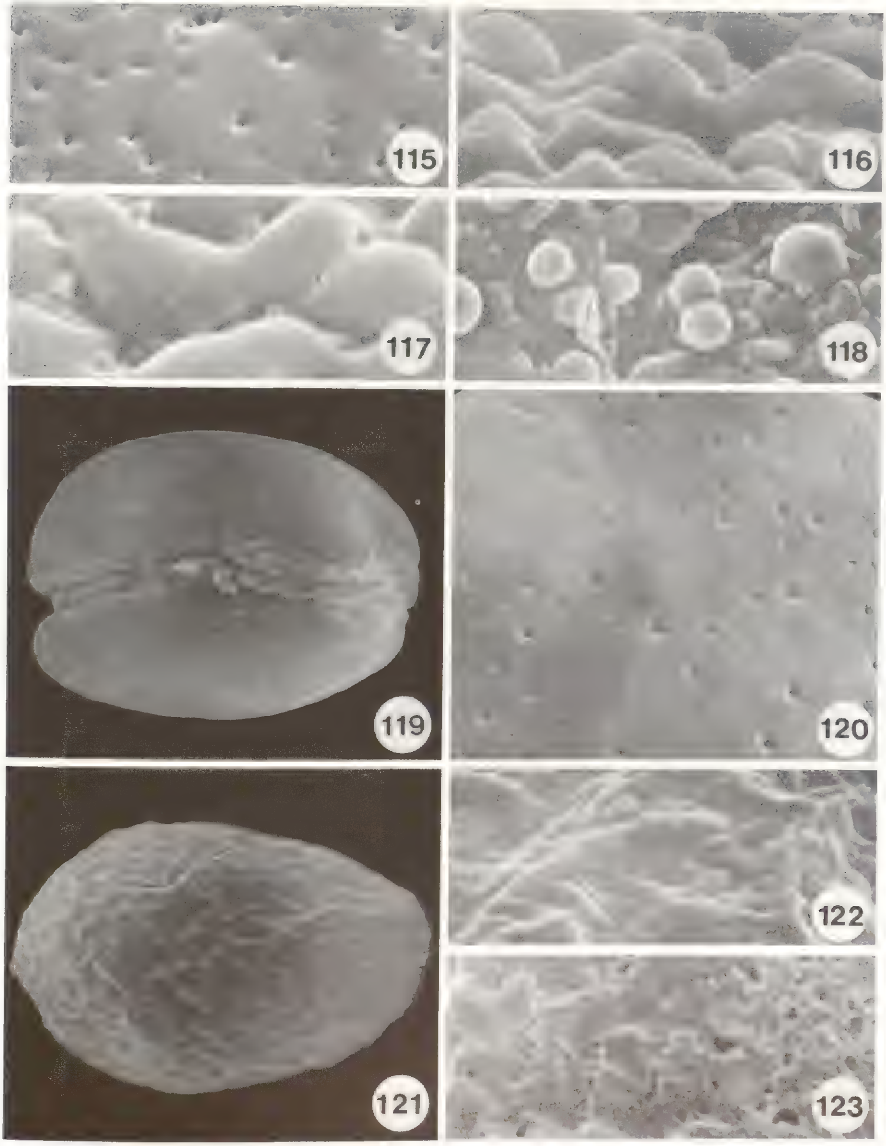
FIGURES 95–100. Pollen of *Amydrium*. 95–98. *A. humile* (PS-177). Fig. 95, ×1,790; Fig. 96, ×1,640. Fig. 97 shows exine surface of pollen half highlighted in Fig. 95; Fig. 98 shows surface of half depicted in Fig. 96. 99, 100. *A. medium* (P-3539). Fig. 99, ×1,785.



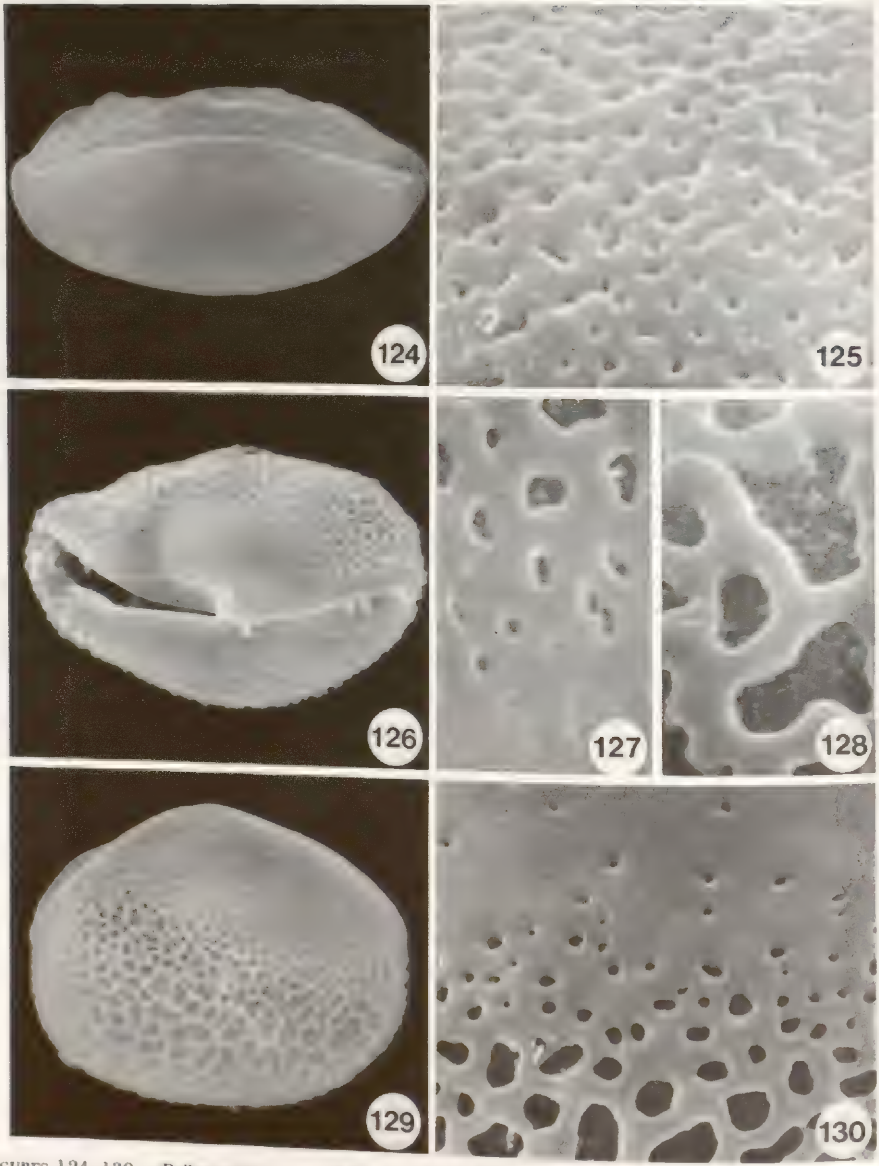
FIGURES 101-108. Pollen of *Epipremnum* (101-104), *Scindapsus* (105, 106) and *Alloschemone* (107, 108). 101-103. *E. pinnatum* (P-3605). Fig. 101, ×2,200; Fig. 102, ×1,880. 104. *E. dahlii* (P-3606). 105, 106. *S. splendidus* (P-3546). Fig. 105, ×1,540. 107, 108. *A. occidentalis* (PS-197). Fig. 107, ×1,380.



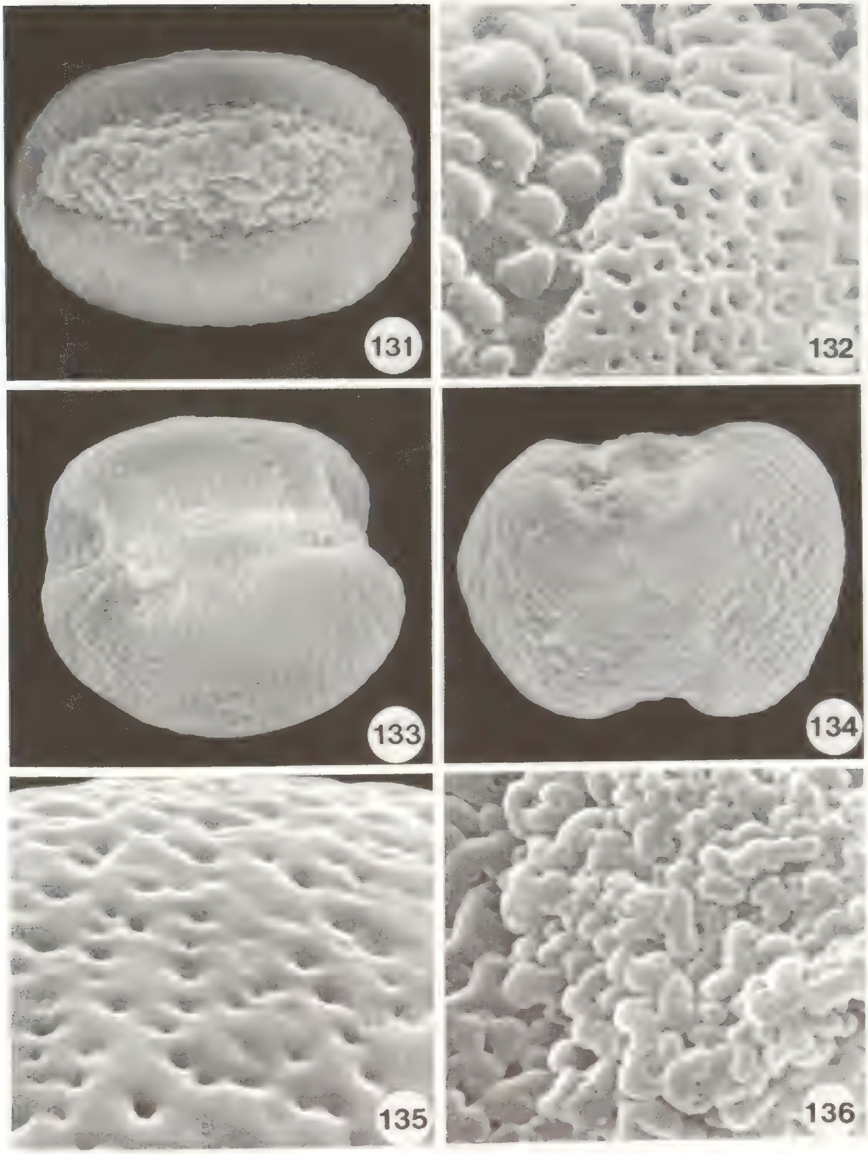
FIGURES 109–114. Pollen of *Stenospermation* (whole grains). 109, 110. *S. angustifolium* (PS-363). Fig. 109, ×1,990; Fig. 110, ×1,880. 111, 112. *S. multiovulatum* (PS-207). Fig. 111, ×1,260; Fig. 112, ×1,190. 113. *S.* sp. indet. (P-3542). ×2,170. 114. *S.* sp. ined. (PS-122). ×1,510.



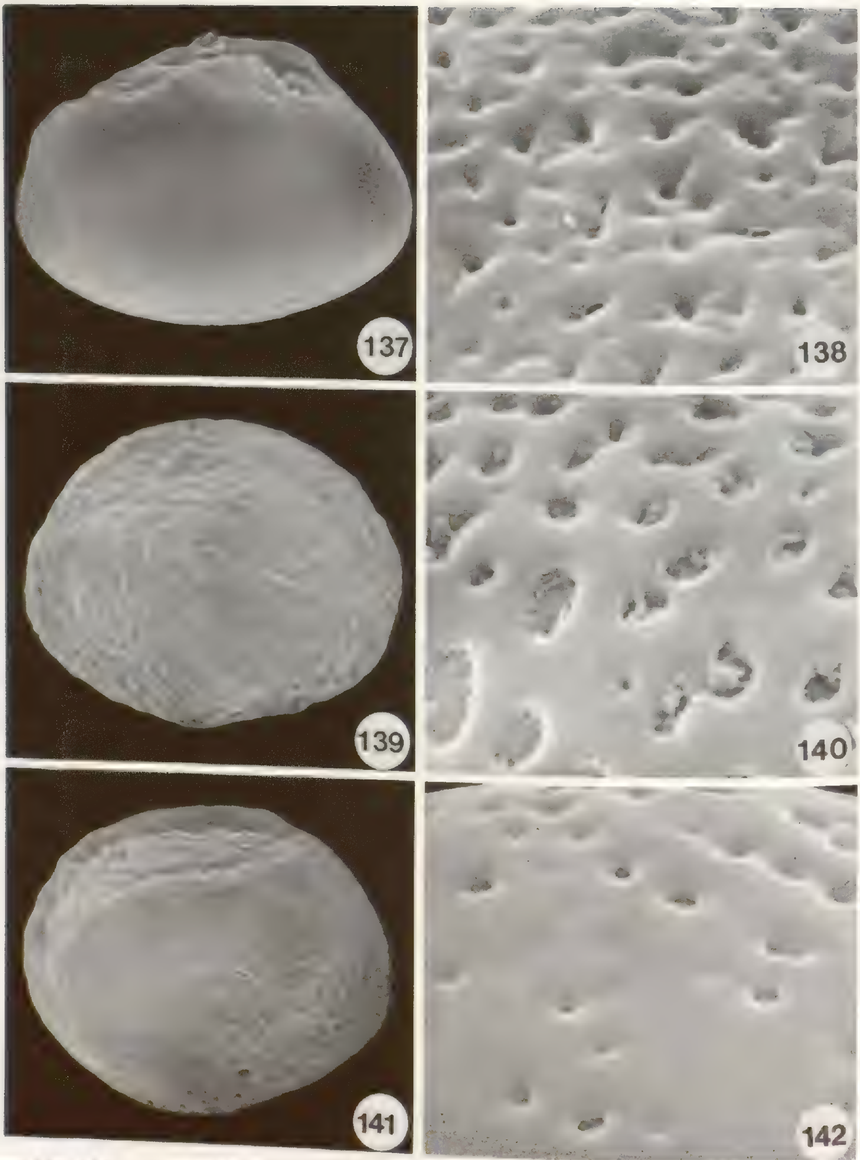
FIGURES 115–123. Pollen of *Stenospermation* (exine surfaces; 115–118) and *Rhodospatha* (119–123). 115. *S. angustifolium* (P-3584). 116. *S.* sp. ined. (PS-122). 117, 118. *S.* sp. indet. (P-3542); showing different portions of the same grain (cf. Fig. 113). 119, 120. *R. oblongata* (PS-416). Fig. 119, ×2,140. 121, 122. *R. pellucida* (PS-370). Fig. 121, ×2,090. 123. *R. venosa* (P-3590).



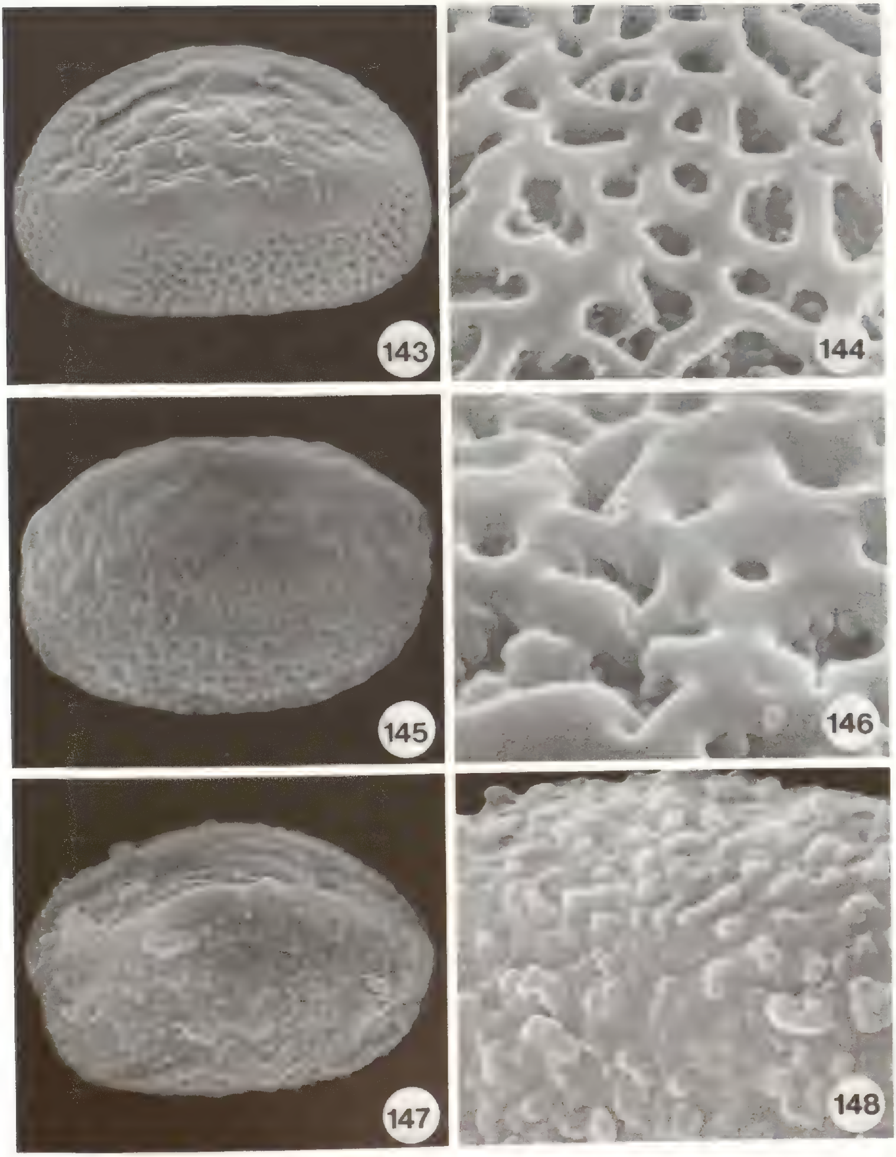
FIGURES 124–130. Pollen of *Orontium* (124, 125) and *Lysichiton* (126–130). 124, 125. *O. aquaticum* (PS-145). Fig. 124, ×1,250. 126–128. *L. camtschatcensis* (PS-477). Fig. 126, ×2,045. Fig. 127 shows transition between reticulate and psilate zones; Fig. 128 shows the coarsest reticulum on the same grain. 129, 130. *L. americanus* (PS-16). Fig. 129, ×1,890. Fig. 130 shows transition between reticulate and psilate zones.



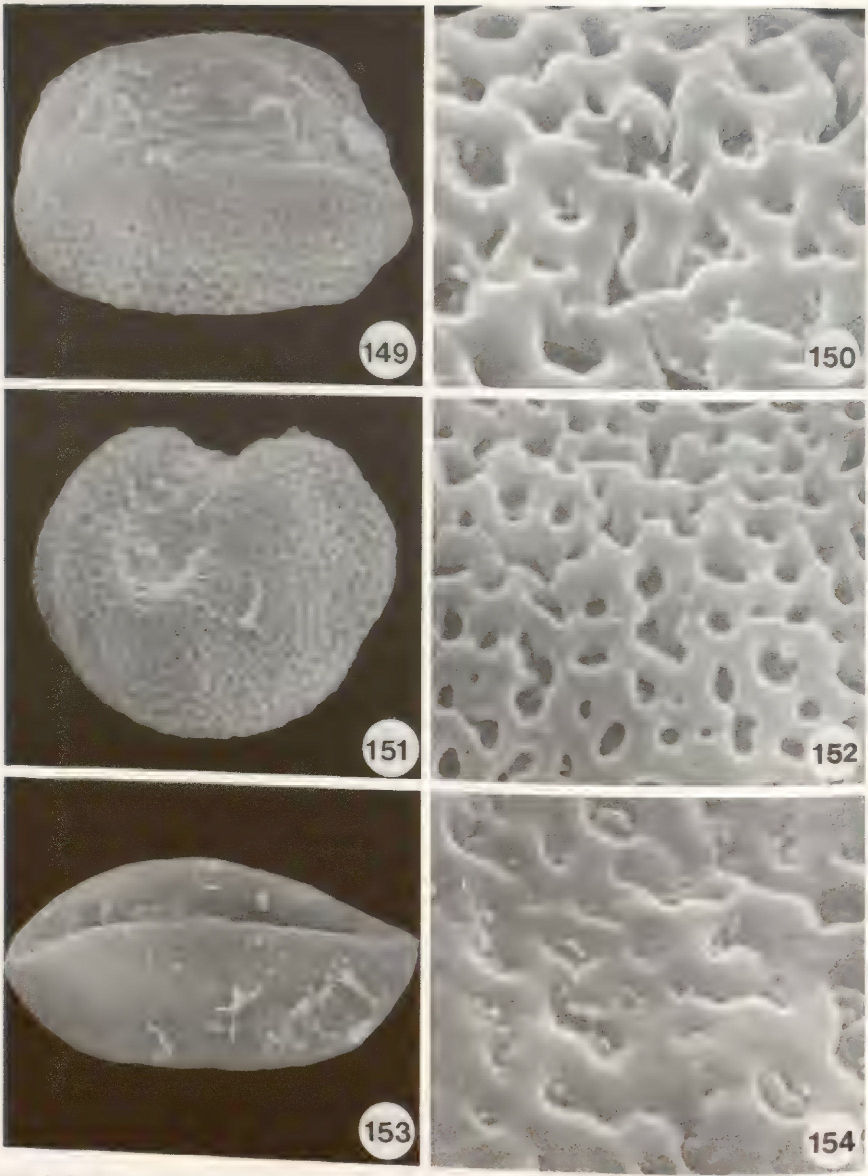
FIGURES 131–136. Pollen of *Symplocarpus* (131, 132) and *Calla* (133–136). 131, 132. *S. foetidus* (PS-22). Fig. 131, ×2,445. Fig. 132 shows a portion of the aperture membrane (to the left) and part of the nonapertural exine surface (to the right). 133–136. *C. palustris* (PS-144). Fig. 133 (×2,590) is presumably an equatorial view of one of the apertures; Fig. 134 (×2,920) is presumably a polar view, with one aperture visible at the top and the position of the other clearly evident at the bottom (see Discussion for clarification). Fig. 135 shows the nonapertural exine surface, Fig. 136 the aperture membrane.



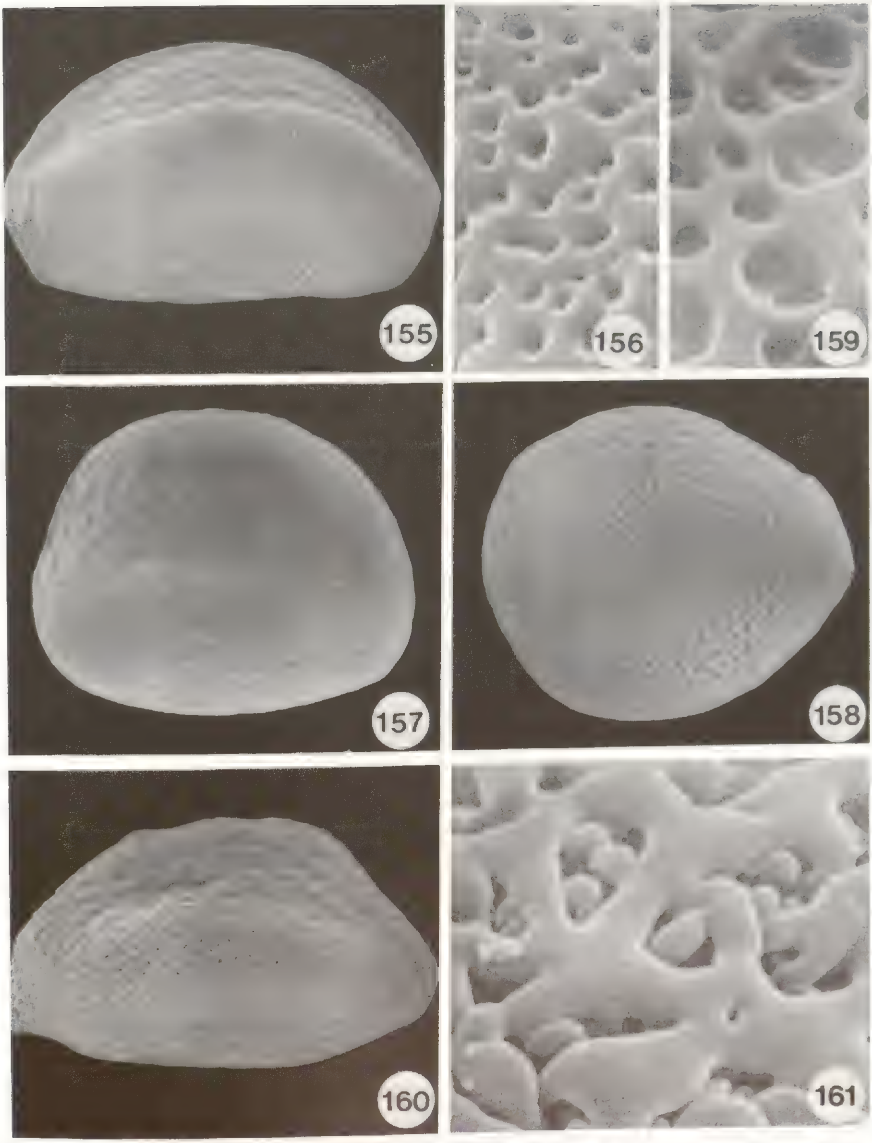
FIGURES 137–142. Pollen of *Cyrtosperma* (137, 138), *Lasimorpha* (139, 140), and *Anaphyllopsis* (141, 142). 137, 138. *C. merkusii* (P-3618). Fig. 137, ×2,440. 139, 140. *L. senegalensis* (P-3620). Fig. 139, ×3,150. 141, 142. *A. americana* (PS-452). Fig. 141, ×2,380.



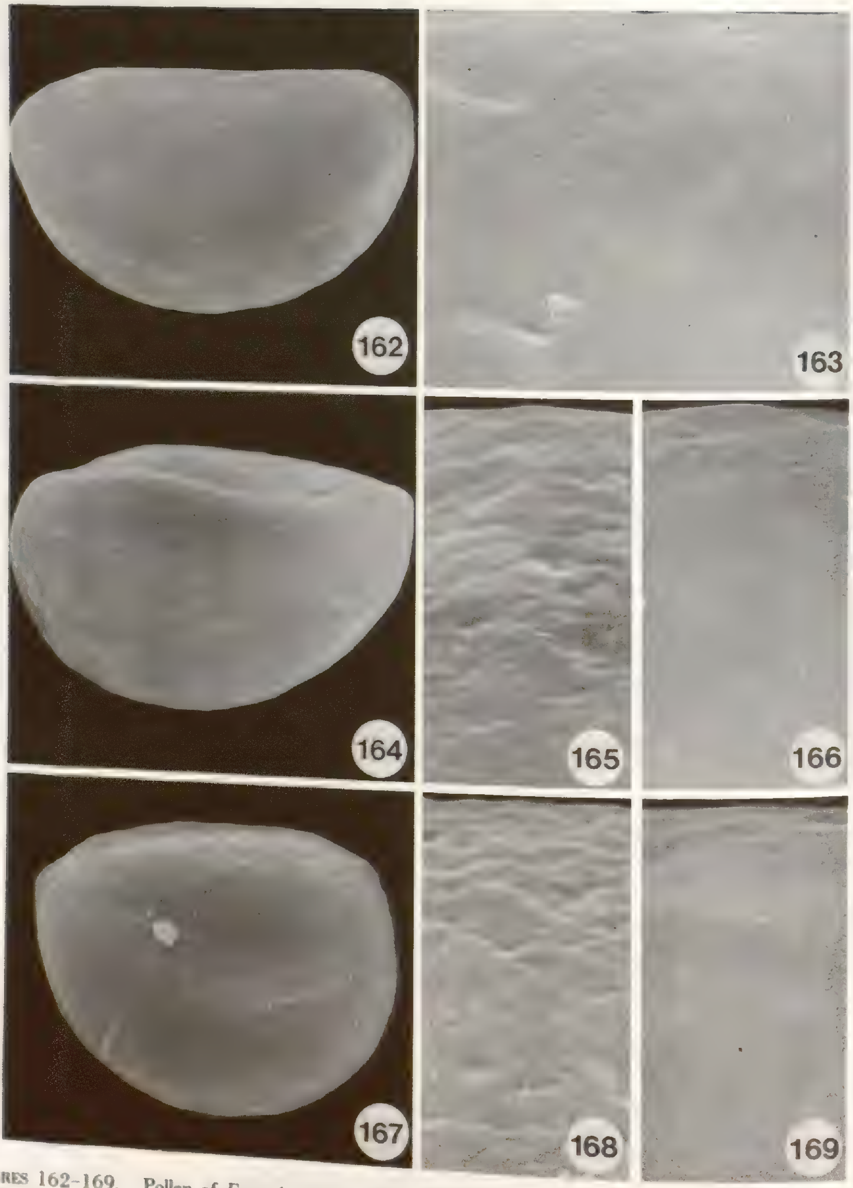
FIGURES 143–148. Pollen of *Lasia* (143, 144), *Anaphyllum* (145, 146), and *Podolasia* (147, 148). 143, 144. *L. spinosa* (P-3621). Fig. 143, ×2,650. 145, 146. *A. wightii* (PS-401). Fig. 145, ×2,130. 147, 148. *P. stipitata* (P-3622). Fig. 147, ×3,870.



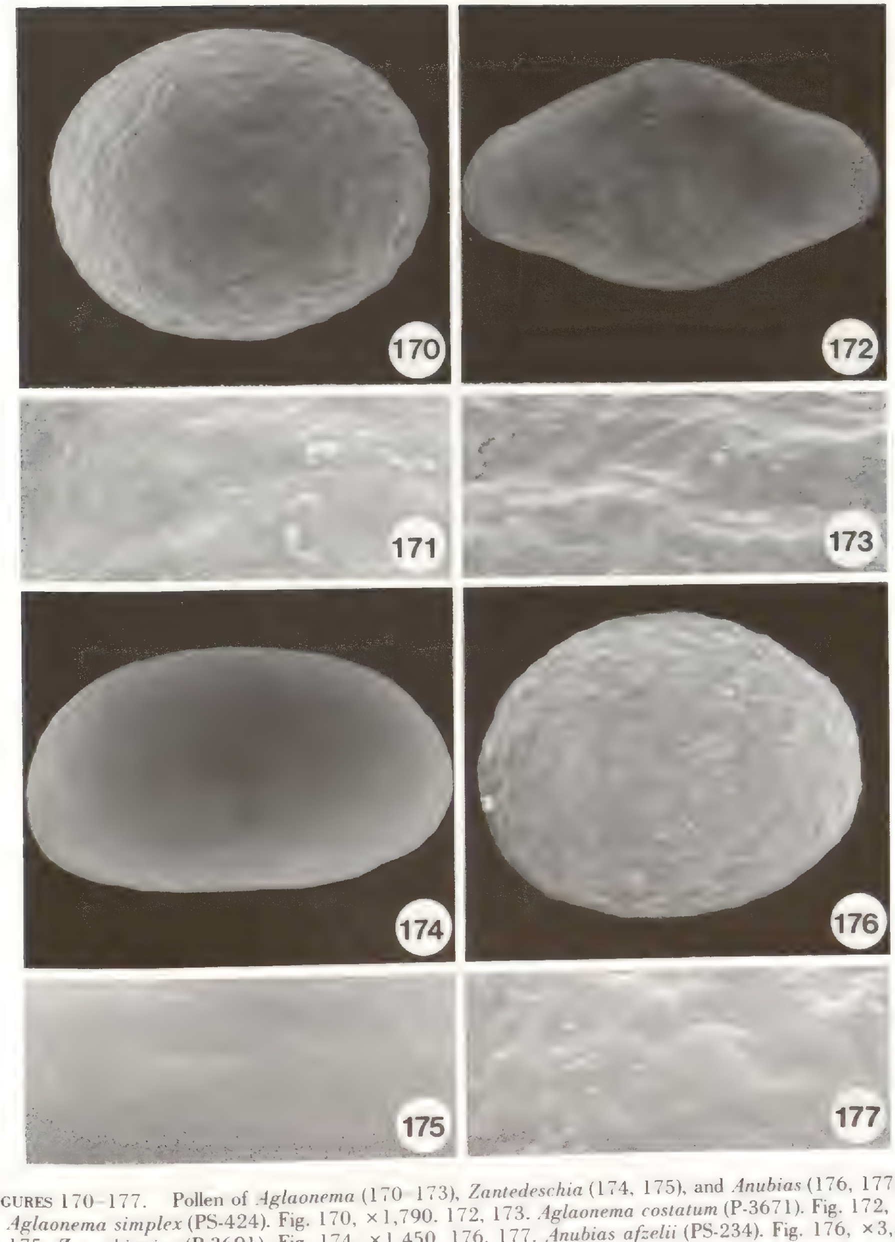
FIGURES 149–154. Pollen of *Urospatha* (149, 150), *Dracontioides* (151, 152), and *Dracontium* pro parte (153, 154). 149, 150. *U. sagittifolia* (P-3624). Fig. 149, ×2,490. 151, 152. *Dracontioides desciscens* (P-3625). Fig. 151 (end view), ×3,250. 153, 154. *Dracontium regelianum* (PS-191). Fig. 153, ×1,645.



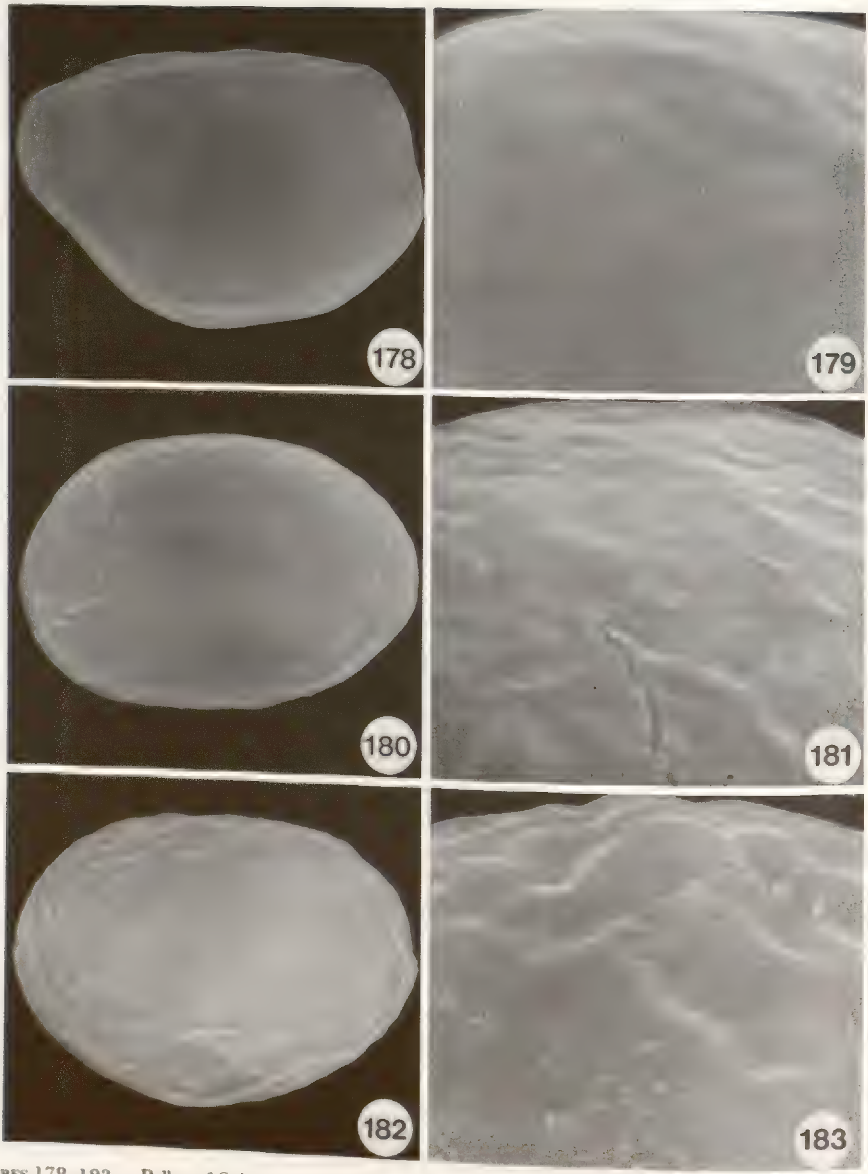
FIGURES 155–161. Pollen of *Dracontium* pro parte (155–159) and *Pycnospatha* (160, 161). 155, 156. *D. asperum* (P-3626). Fig. 155, ×2,270. 157–159. *D. polyphyllum* (PS-273). Fig. 157 (apertural face), ×2,180; Fig. 158 (nonapertural face), ×1,860. Fig. 159 shows the coarsest reticulum near center of the nonapertural face. 160, 161. *P. arietina* (PS-415). Fig. 160, ×2,170.



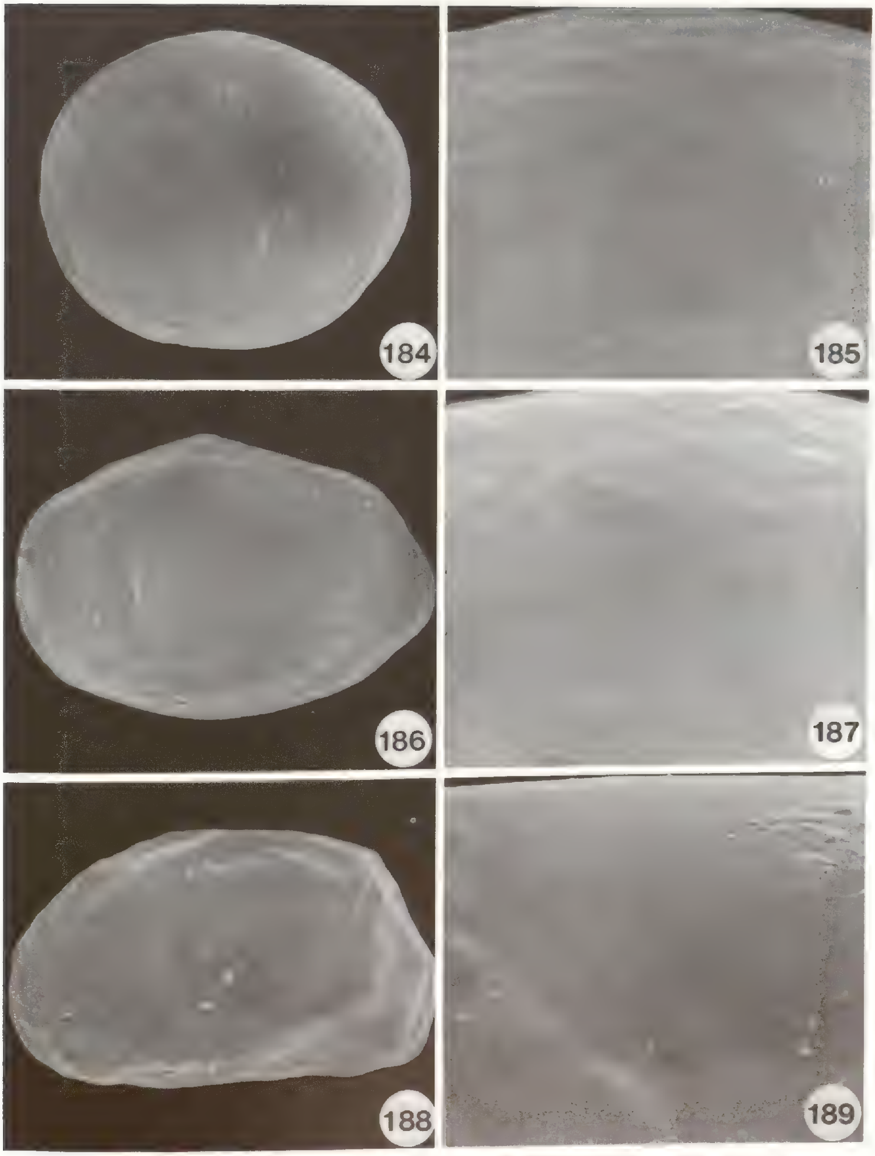
FIGURES 162–169. Pollen of *Furtadoa* (162, 163) and *Homalomena* (164–169). 162, 163. *F. sumatrensis* (PS-458). Fig. 162, ×4,660. 164, 165. *H. propinqua* (P-3657). Fig. 164, ×2,260. 166. *H. lindenii* (P-3656). 167, 168. *H. wallisii* (PS-162). Fig. 167, ×2,595. 169. *H. speariae* (PS-268).



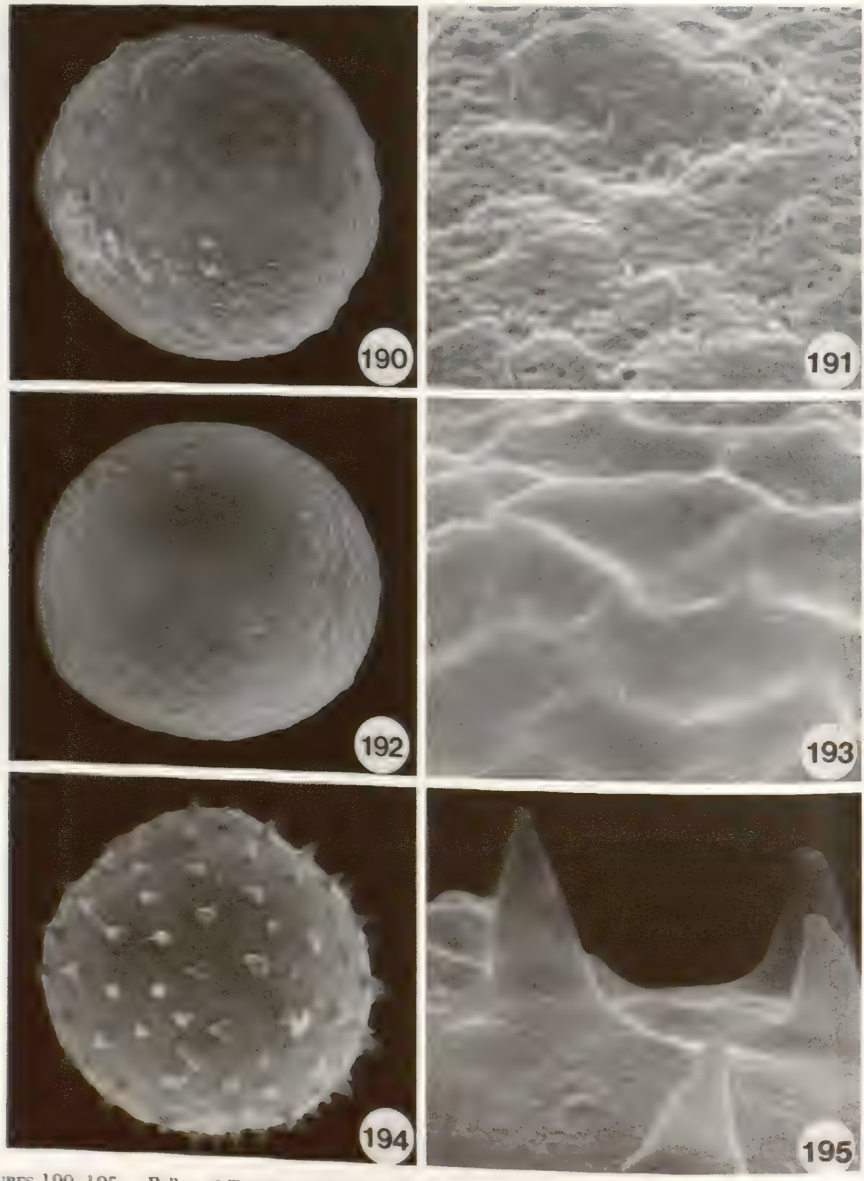
Figures 170–177. Pollen of *Aglaonema* (170–173), *Zantedeschia* (174, 175), and *Anubias* (176, 177). 170, 171. *Aglaonema simplex* (PS-424). Fig. 170, ×1,790. 172, 173. *Aglaonema costatum* (P-3671). Fig. 172, ×970. 174, 175. *Z. aethiopica* (P-3691). Fig. 174, ×1,450. 176, 177. *Anubias afzelii* (PS-234). Fig. 176, ×3,510.



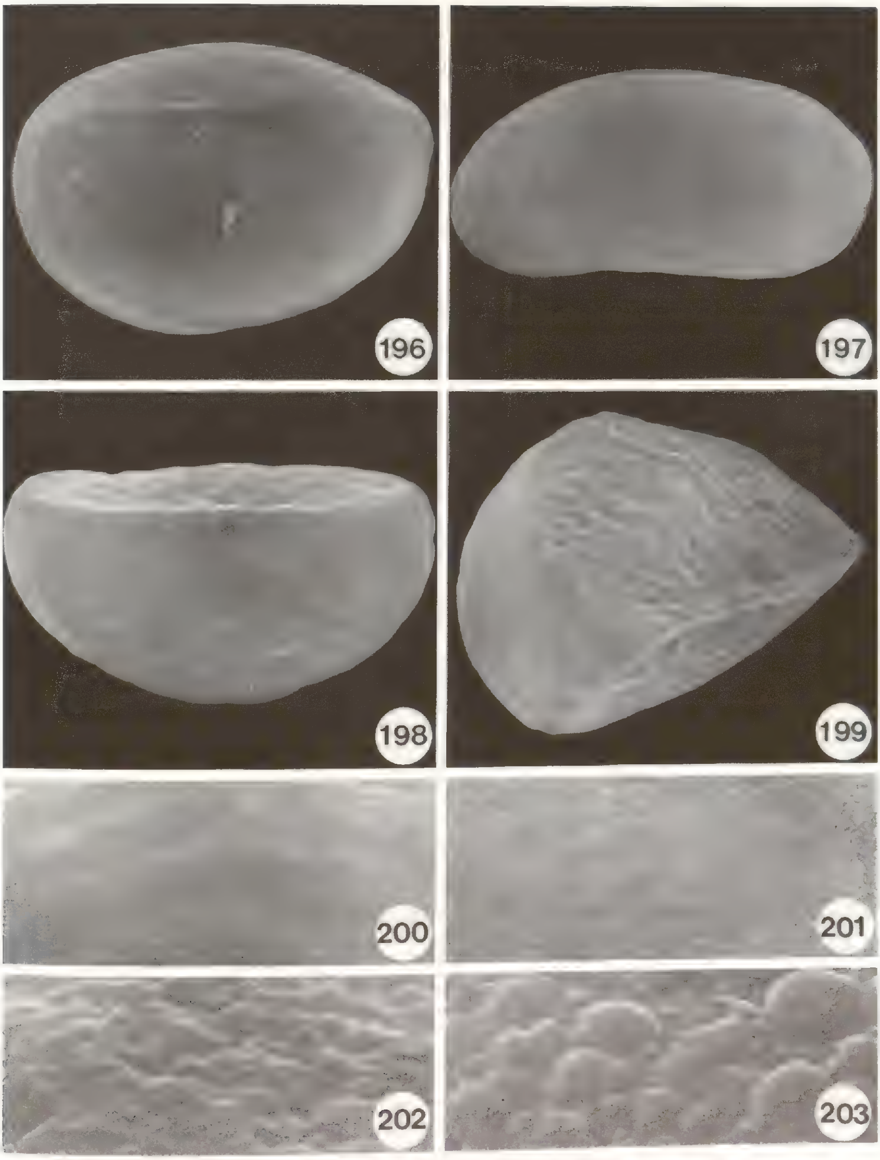
FIGURES 178–183. Pollen of *Schismatoglottis* (178–181) and *Piptospatha* (182, 183). 178, 179. *S. calyptrata* (P-3555). Fig. 178, ×4,180. 180, 181. *S. spruceana* (PS-485). Fig. 180, ×2,700. 182, 183. *P. elongata* (P-3664). Fig. 182, ×3.105.



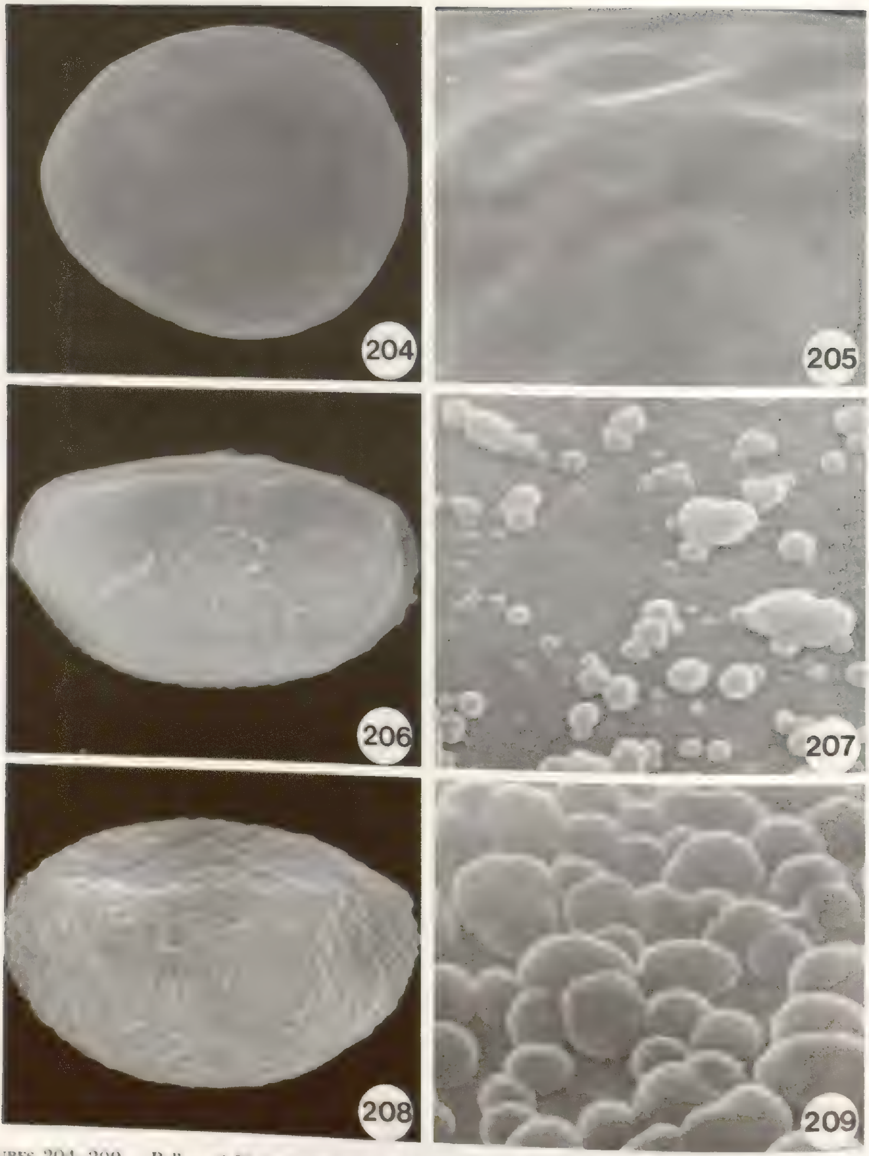
FIGURES 184–189. Pollen of *Phymatarum* (184, 185), *Aridarum* (186, 187), and *Hottarum* (188, 189). 184, 185. *P. borneense* (PS-140). Fig. 184, ×2,980. 186, 187. *A. nicolsonii* (PS-150). Fig. 186, ×4,030. 188, 189. *H. sarikeense* (PS-171). Fig. 188, ×4,640.



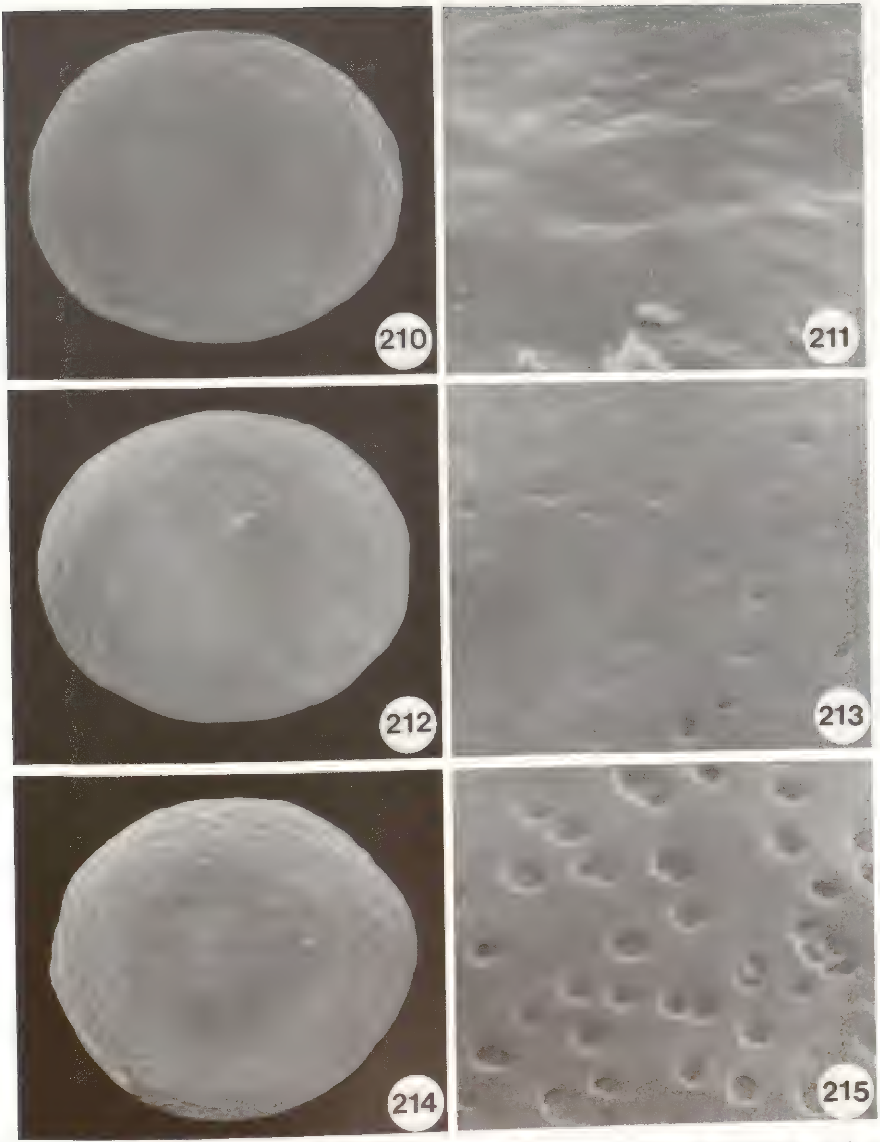
Figures 190–195. Pollen of *Typhonodorum* (190, 191) and *Peltandra* (192–195). 190, 191. *T. lindleyanum* (PS-507). Fig. 190, ×1,360. 192, 193. *P. sagittifolia* (P-3689). Fig. 192, ×1,680. 194, 195. *P. virginica* (PS-20). Fig. 194, × 2,040.



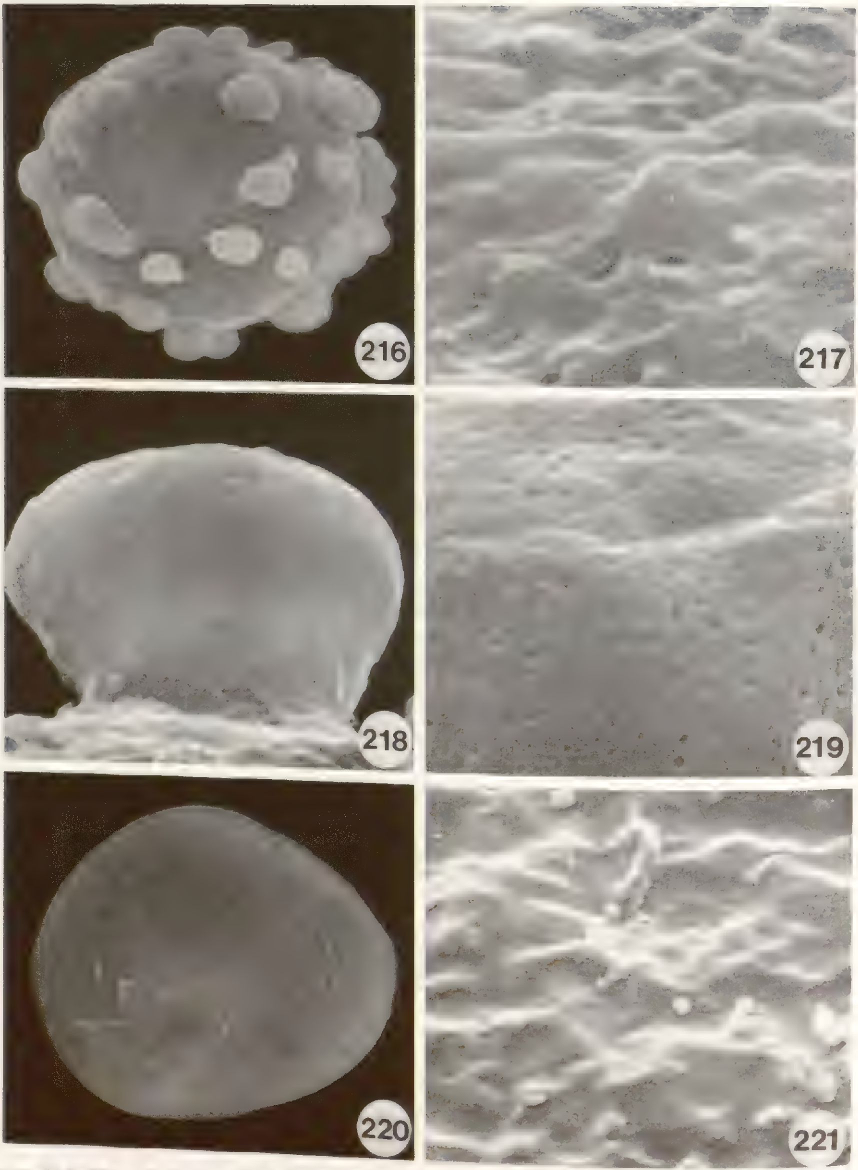
FIGURES 196–203. Pollen of *Philodendron* subg. *Philodendron* (196, 198–203) and subg. *Pteromischum* (197). 196. *P. jodavisianum* (PS-392). ×2,180. 197. *P. rhodoaxis* (PS-113). ×2,470. 198, 199. *P. callosum* (PS-163). Fig. 198 (×2,480) shows both proximal faces; Fig. 199 (×2,870) shows both proximal faces plus a portion of the distal face (at left). 200. *P. radiatum* (PS-111). 201. *P. fragrantissimum* (PS-389). 202. *P. wendlandii* (PS-367). 203. *P. rugosum* (PS-446).



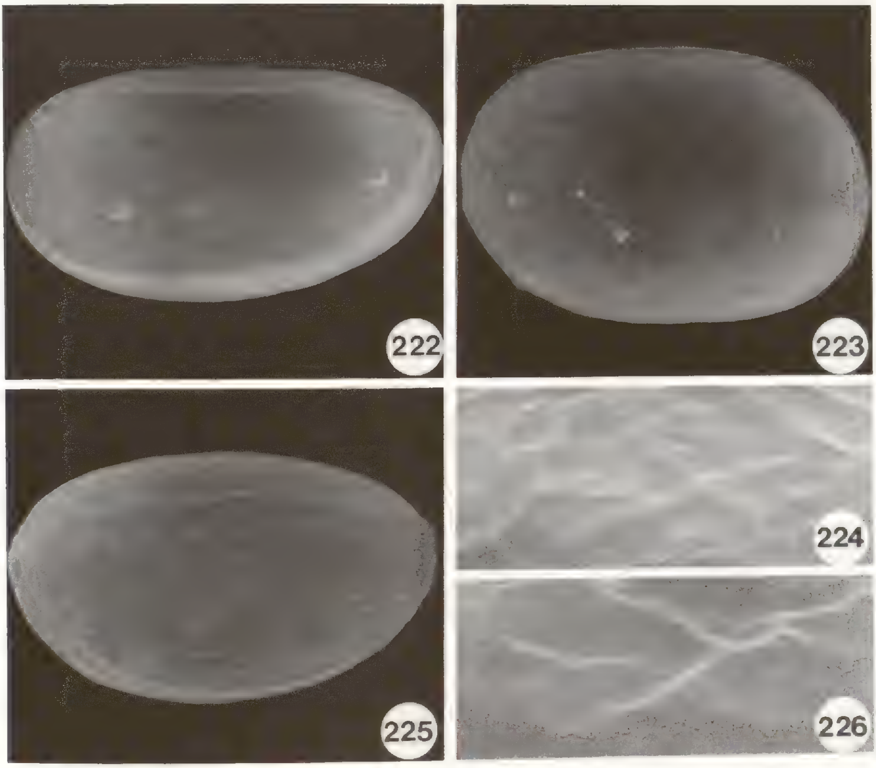
FIGURES 204–209. Pollen of *Philodendron* subg. *Meconostigma*. 204, 205. *P. bipinnatifidum* (P-3778). Fig. 204, ×1,270. 206, 207. *P. goeldii* (PS-437). Fig. 206, ×1,440. 208, 209. *P. leal-costae* (PS-410). Fig. 208, ×1,785.



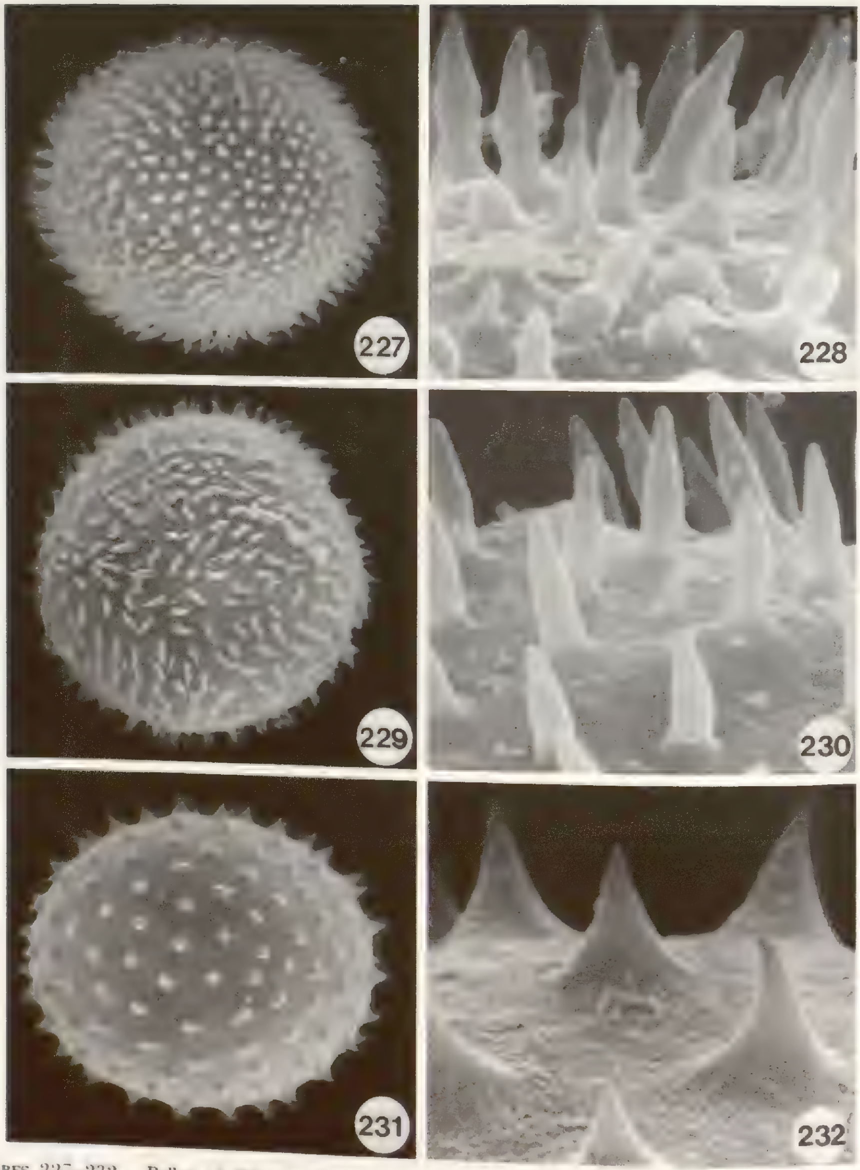
FIGURES 210–215. Pollen of *Dieffenbachia* pro parte. 210, 211. *D.* cf. *herthae* (P-3685). Fig. 210, ×1,050. 212, 213. *D. picta* var. *barraquiniana* (P-3688). Fig. 212, ×950. 214, 215. *D. pittieri* (P-3683). Fig. 214, ×1,030.



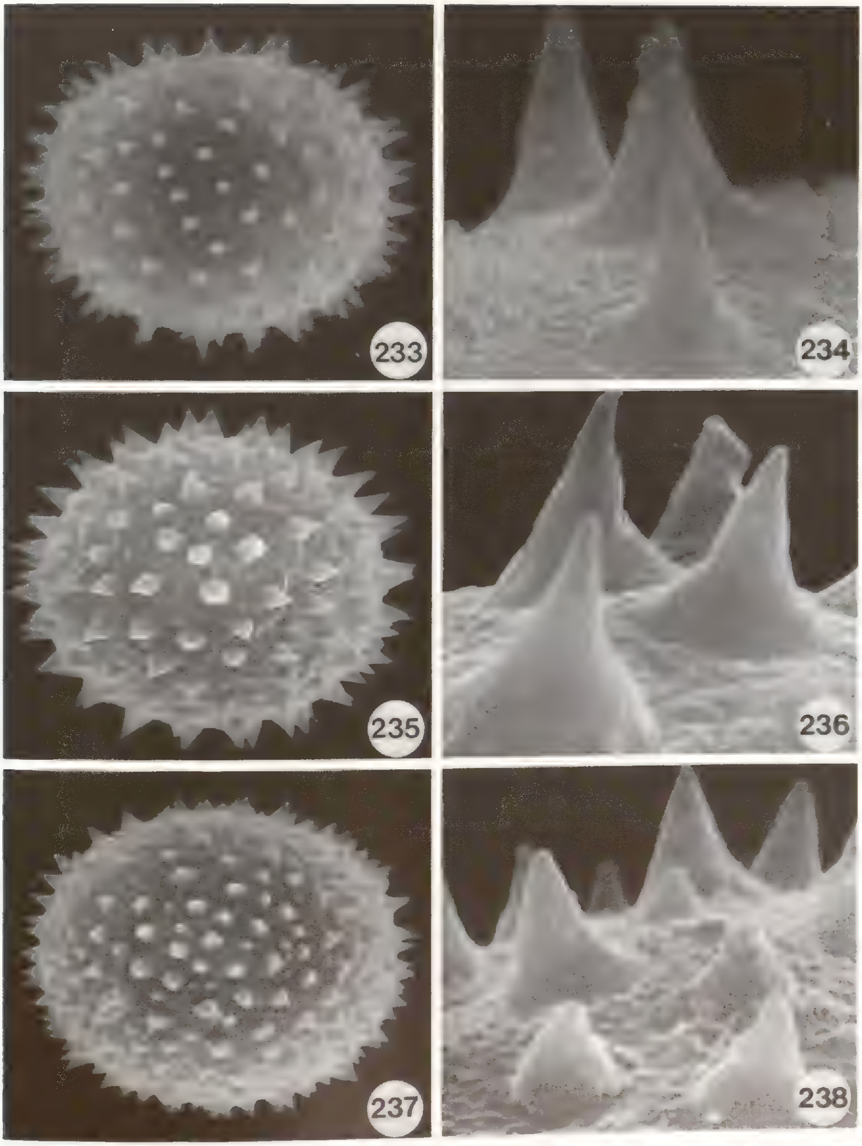
FIGURES 216–221. Pollen of *Dieffenbachia* pro parte (216–219) and *Bognera* (220, 221). 216–219. *D. parlatorei* (P-3686). Fig. 216, ×680. Fig. 217 shows the exine surface between the tubercles; Fig. 218 (×4,550) is a close-up of a single tubercle, and Fig. 219 shows the exine surface of the tubercle itself (cf. Figs. 300–303). 220, 221. *B. recondita* (PS-202). Fig. 220, ×1,290.



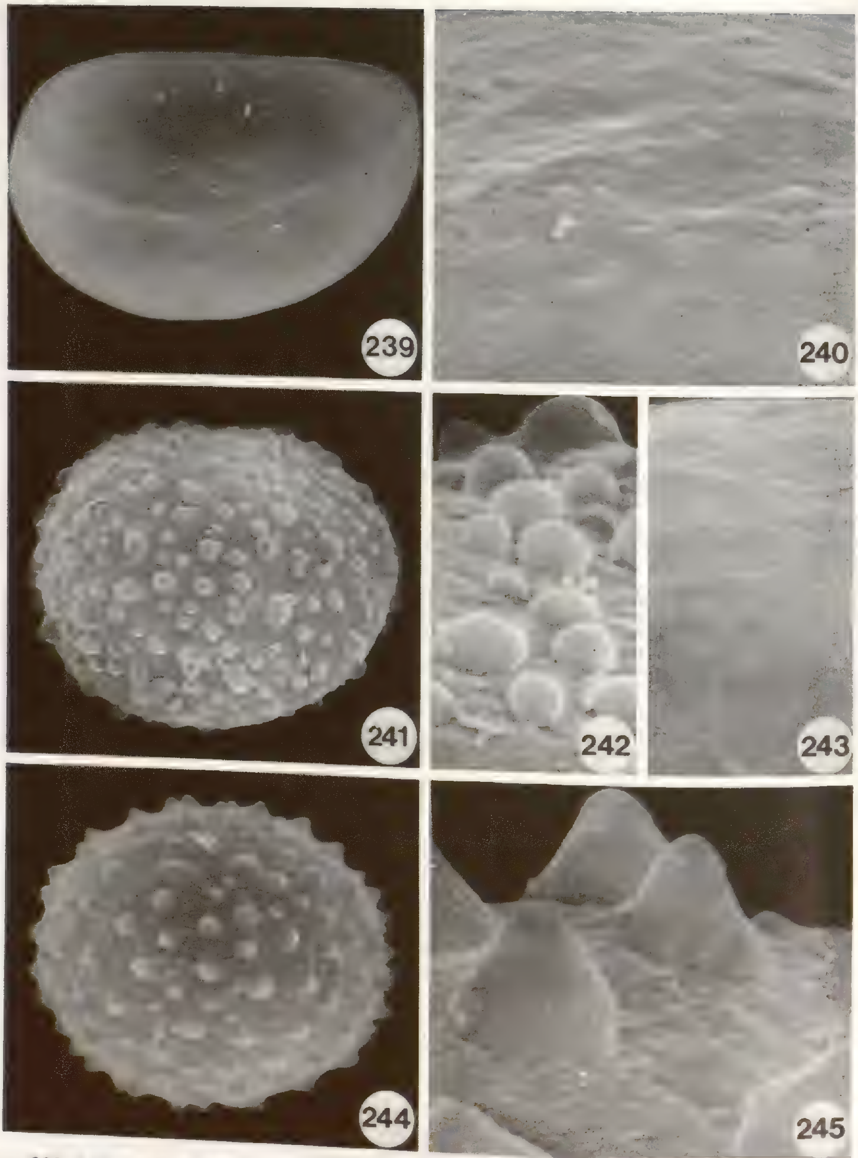
FIGURES 222–226. Pollen of *Cryptocoryne* (222–224) and *Lagenandra* (225, 226) (subtribe Cryptocoryninae). 222. *C. affinis* (PS-189). ×2,200. 223, 224. *C. albida* (P-3750). Fig. 223, ×1,990. 225, 226. *L. toxicaria* (P-3749). Fig. 225, ×1,710.



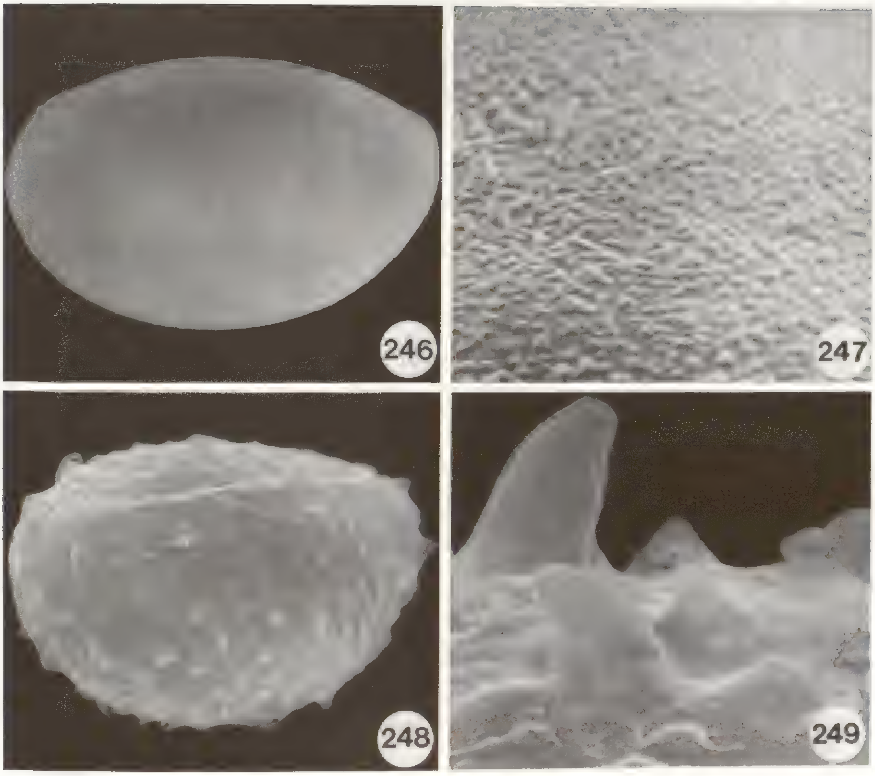
FIGURES 227–232. Pollen of *Filarum* (227, 228), *Ulearum* (229, 230), and *Zomicarpa* (231, 232) (tribe Zomicarpeae). 227, 228. *F. manserichense* (P-3730). Fig. 227, ×2,130. 229, 230. *U. sagittatum* (P-3711). Fig. 229, ×1,760. 231, 232. *Z. riedeliana* (PS-291). Fig. 231, ×1,880.



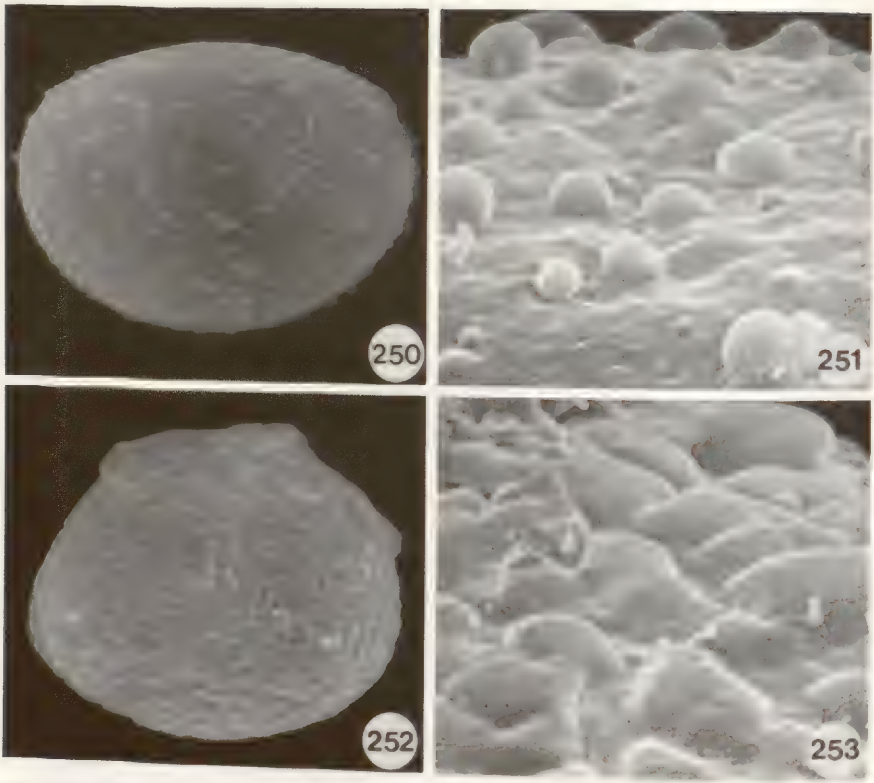
FIGURES 233–238. Pollen of *Carlephyton* (233, 234), *Colletogyne* (235, 236), and *Arophyton* (237, 238) (tribe Arophyteae). 233, 234. *Carlephyton madagascariense* (PS-285). Fig. 233, ×1,695. 235, 236. *Colletogyne perrieri* (PS-135). Fig. 235, ×1,680. 237, 238. *A. buchetii* (P-3564). Fig. 237, ×1,820.



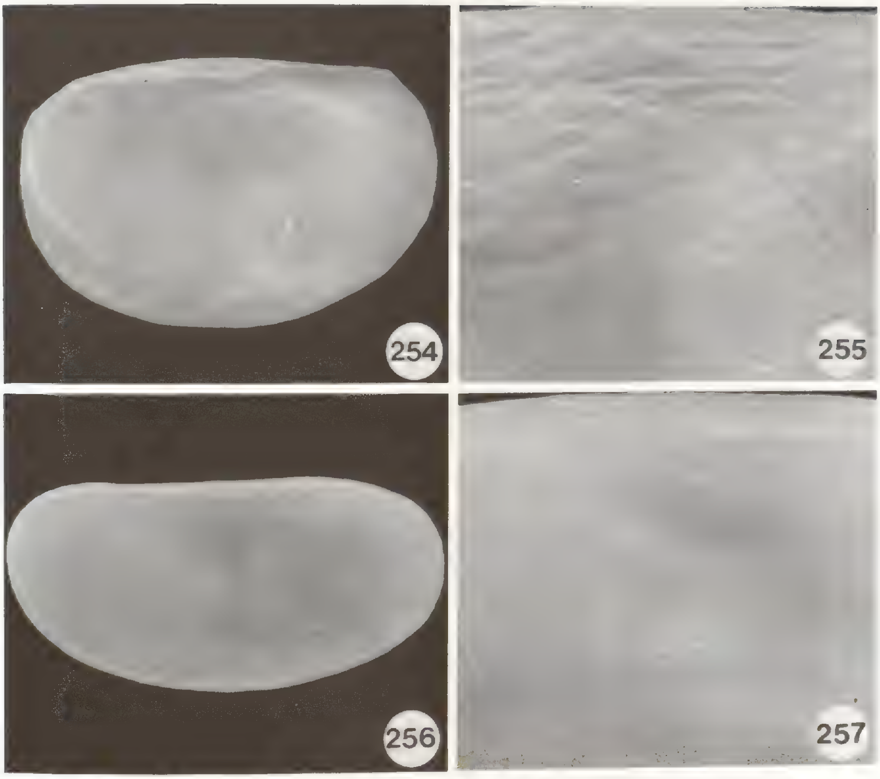
FIGURES 239–245. Pollen of *Asterostigma* (239–243) and *Synandrospadix* (244, 245). 239, 240. *A. riedelianum* (PS-439). Fig. 239, ×1,910. 241, 242. *A. pavonii* (PS-438). Fig. 241, ×2,760. 243. *A. lividum* (PS-267). 244, 245. *S. vermitoxicus* (P-3567). Fig. 244, ×1,540.



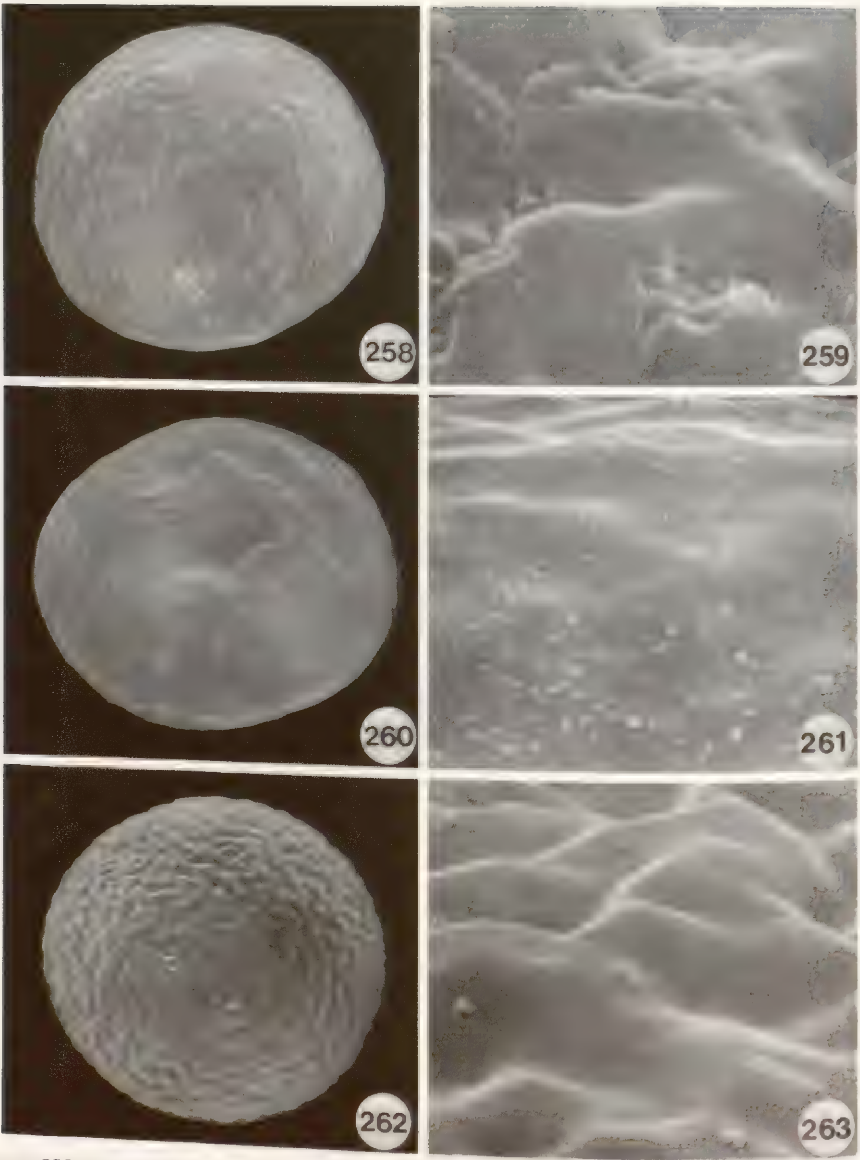
FIGURES 246–249. Pollen of *Taccarum*. 246, 247. *T. weddellianum* (PS-143). Fig. 246, ×1,420. 248, 249. *T. cardenasianum* (P-3565). Fig. 248, ×1,600.



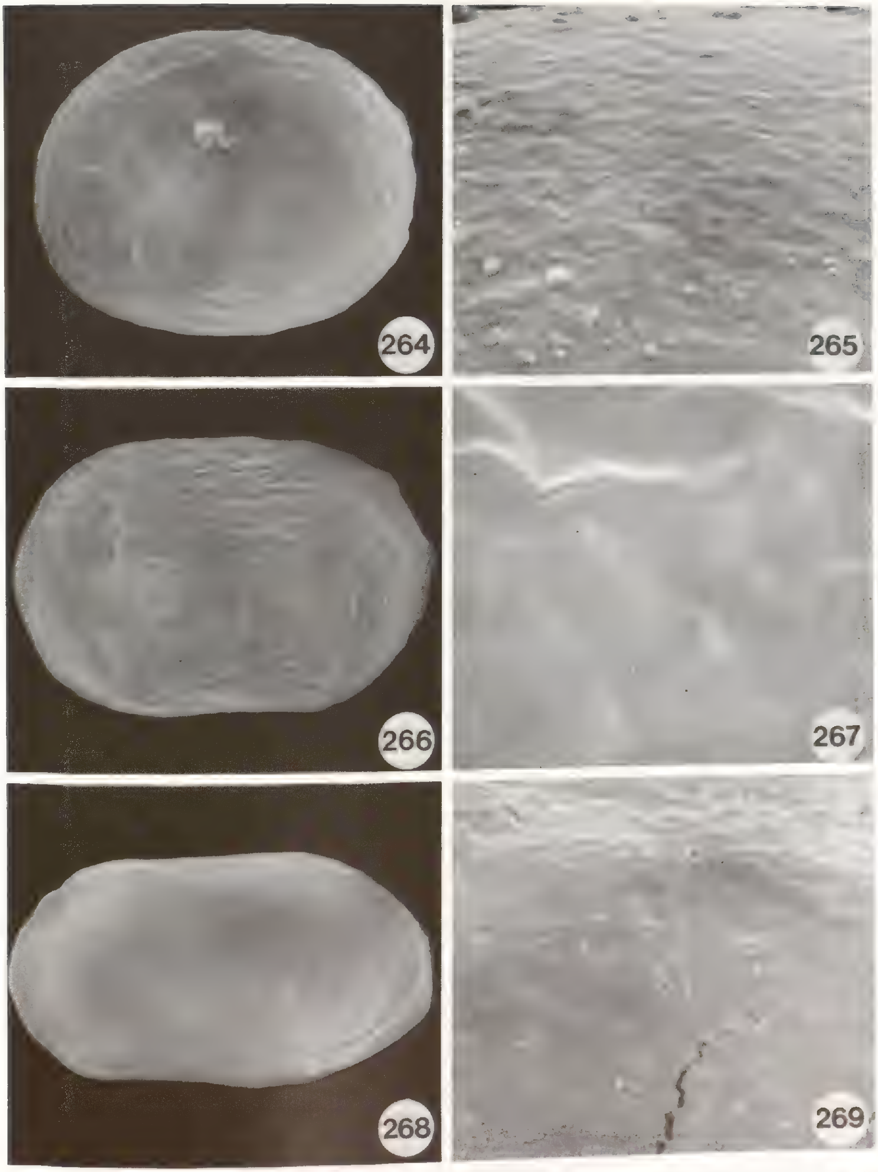
FIGURES 250–253. Pollen of *Gorgonidium*. 250, 251. *G. mirabile* (P-3534). Fig. 250, ×1,630. 252, 253. *G. vargasii* (PS-459). Fig. 252, ×1,880.



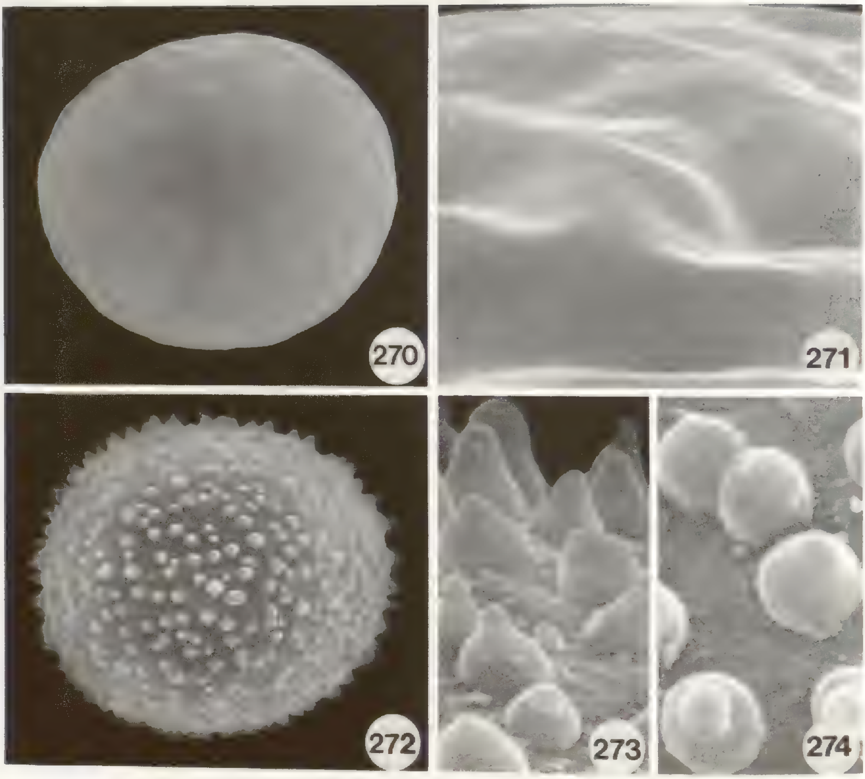
FIGURES 254–257. Pollen of *Spathantheum* (254, 255) and *Spathicarpa* (256, 257). 254, 255. *Spathantheum orbignyanum* (P-3568). Fig. 254, ×1,900. 256, 257. *Spathicarpa sagittifolia* (P-3729). Fig. 256, ×1,800.



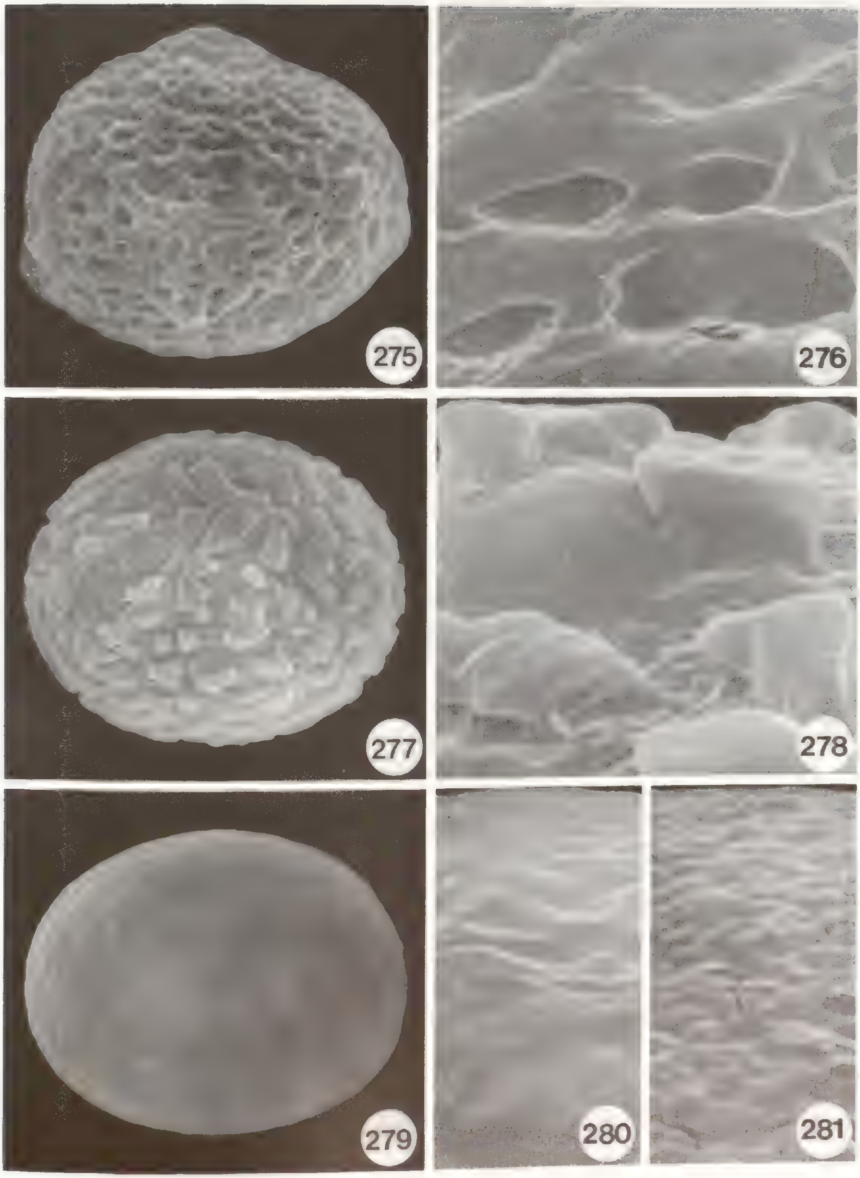
Figures 258–263. Pollen of *Cercestis* (258–261) and *Nephthytis* (262, 263) (tribe Nephthytideae). 258, 259. *C. stigmaticus* (PS-408). Fig. 258, ×1,230. 260, 261. *C. mirabilis* (P-3647). Fig. 260, ×1,330. 262, 263. *N. afzelii* (PS-240). Fig. 262, ×1,190.



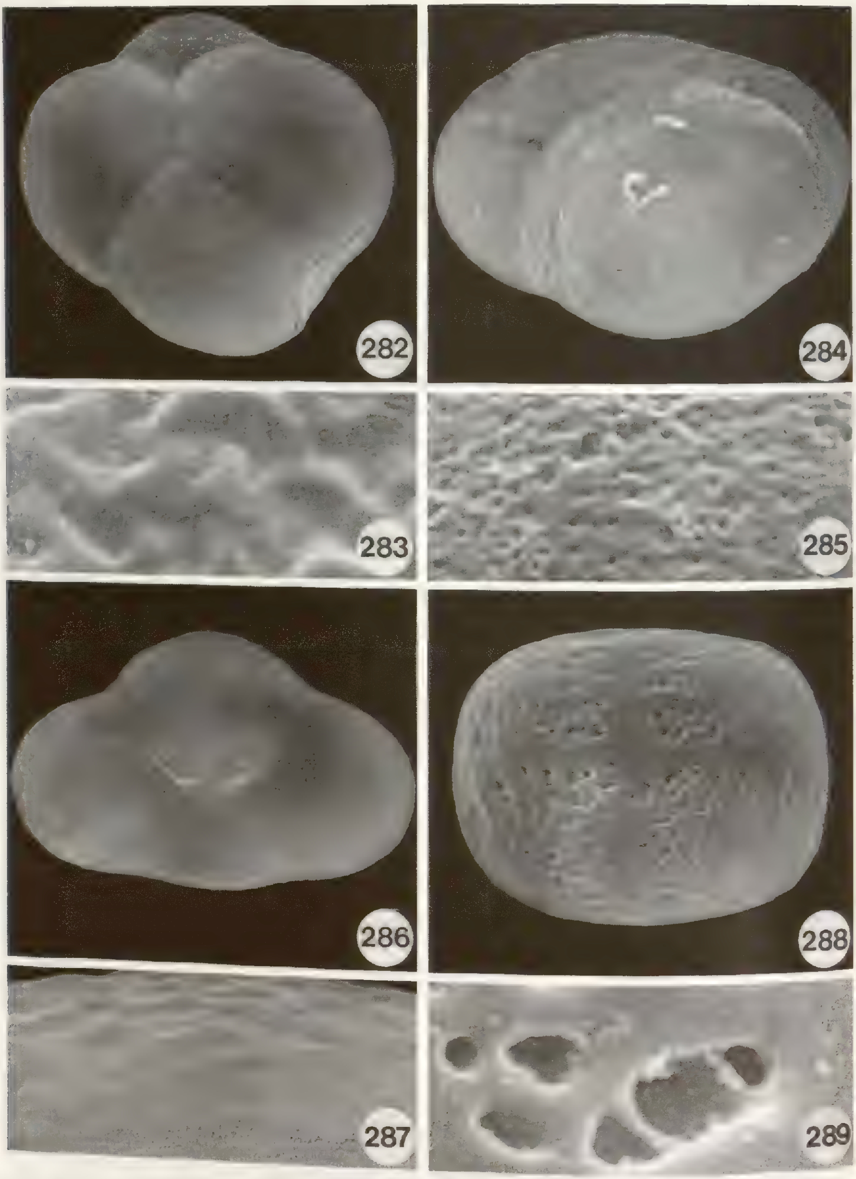
FIGURES 264–269. Pollen of *Anchomanes* (264–267) and *Pseudohydrosme* (268, 269). 264. *A.* sp. indet. (P-3629). ×1,050. 265. *A. difformis* (PS-152). 266, 267. *A. nigritianus* (PS-494). Fig. 266, ×830. 268, 269. *P. gabunensis* (PS-414). Fig. 268, ×480.



FIGURES 270–274. Pollen of *Montrichardia* (270, 271) and *Callopsis* (272–274). 270, 271. *M. arborescens* (P-3553). Fig. 270, ×760. 272–274. *Callopsis volkensii* (PS-159). Fig. 272, ×1,880.



FIGURES 275–281. Pollen of *Jasarum* (275, 276), *Scaphispatha* (277, 278), and *Caladium* (279–281). 275, 276. *J. steyermarkii* (P-3708). Fig. 275, ×1,630. 277, 278. *S. gracilis* (P-3571). Fig. 277, ×1,730. 279, 280. *C. bicolor* (PS-107). Fig. 279, ×1,795. 281. *C. tuberosum* (PS-175).



FIGURES 282–289. Pollen of *Xanthosoma* (282–285) and *Chlorospatha* (286–289). 282, 283. *X. striatipes* (PS-434). Fig. 282 (tetrad), ×770. 284, 285. *X. pilosum* (PS-398). Fig. 284 (tetrad), ×1,110. 286, 287. *C. corrugata* (PS-134). Fig. 286 (tetrad), ×1,400. 288, 289. *C. croatiana* subsp. *croatiana* (PS-249). Fig. 288 (tetrad), ×1,510.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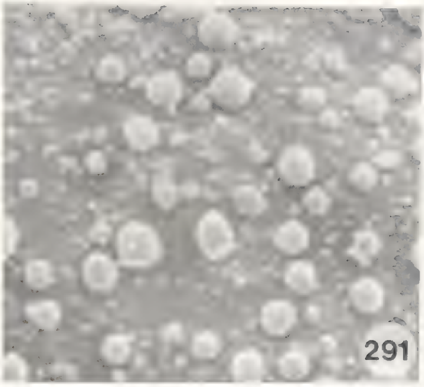
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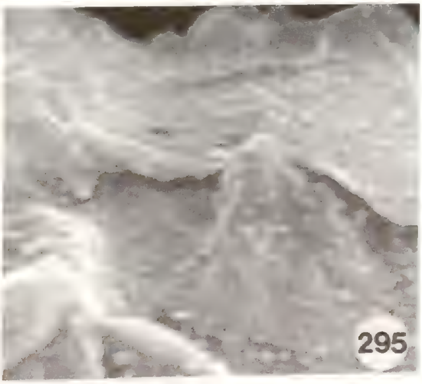
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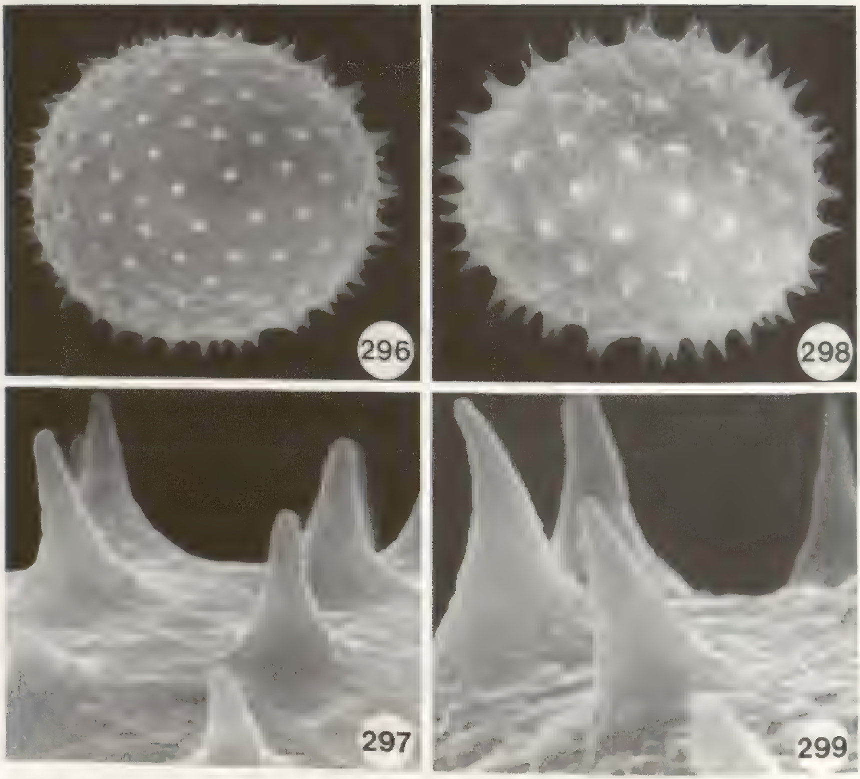
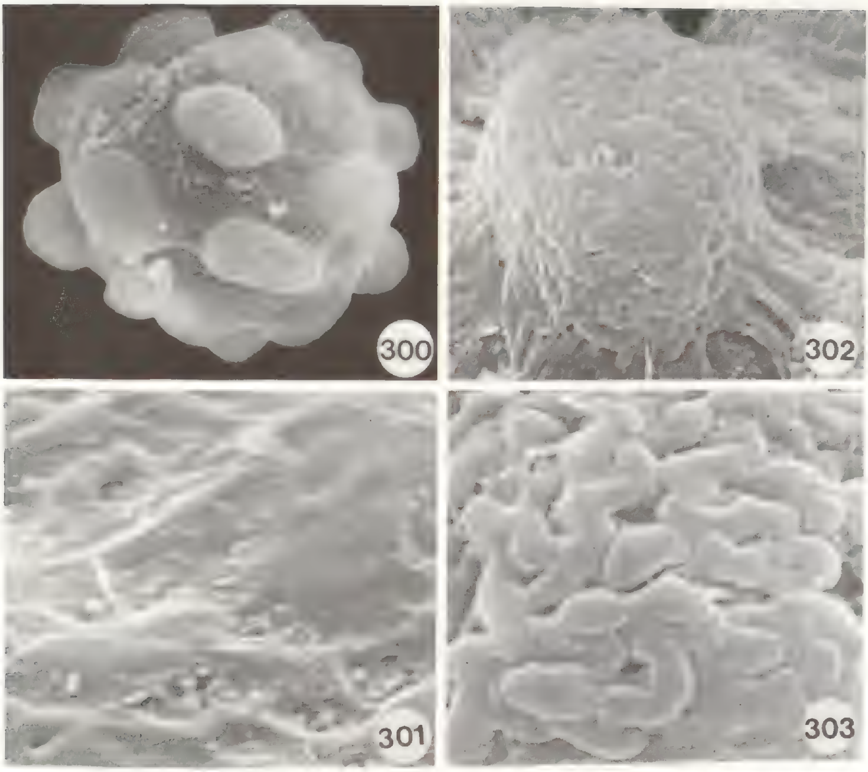
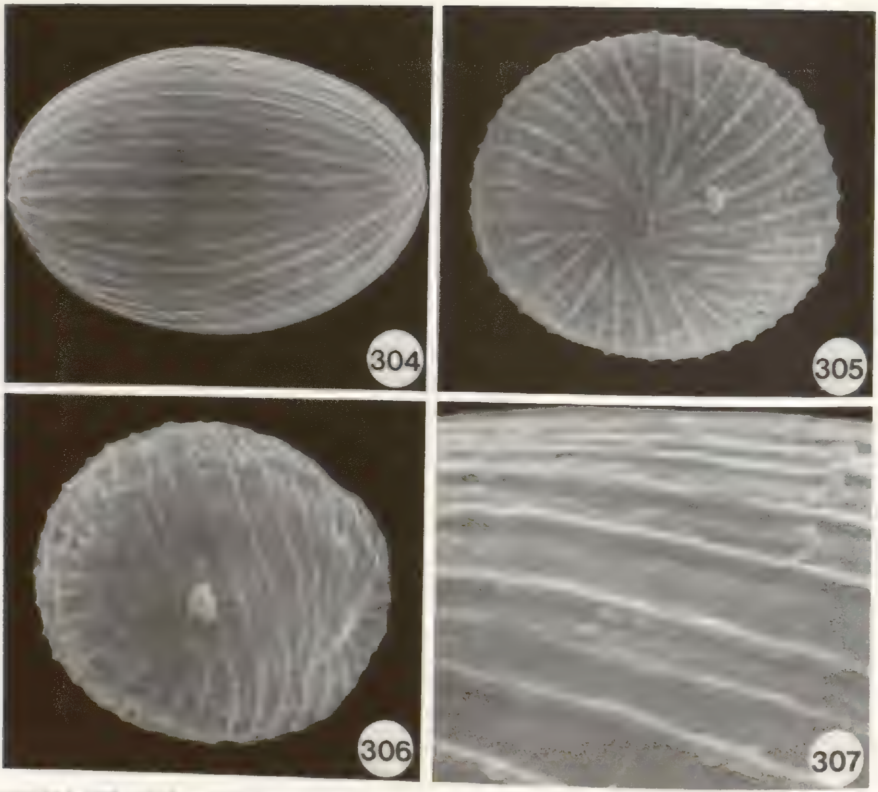
FIGURES 290–295. Pollen of *Syngonium* (species with subpsilate, verruculate, or rugulate exine). 290, 291. *S. schottianum* (PS-205). Fig. 290, ×1,050. 292, 293. *S. birdseyanum* (PS-427). Fig. 292, ×1,230. 294, 295. *S. neglectum* (P-3710). Fig. 294, ×1,065.



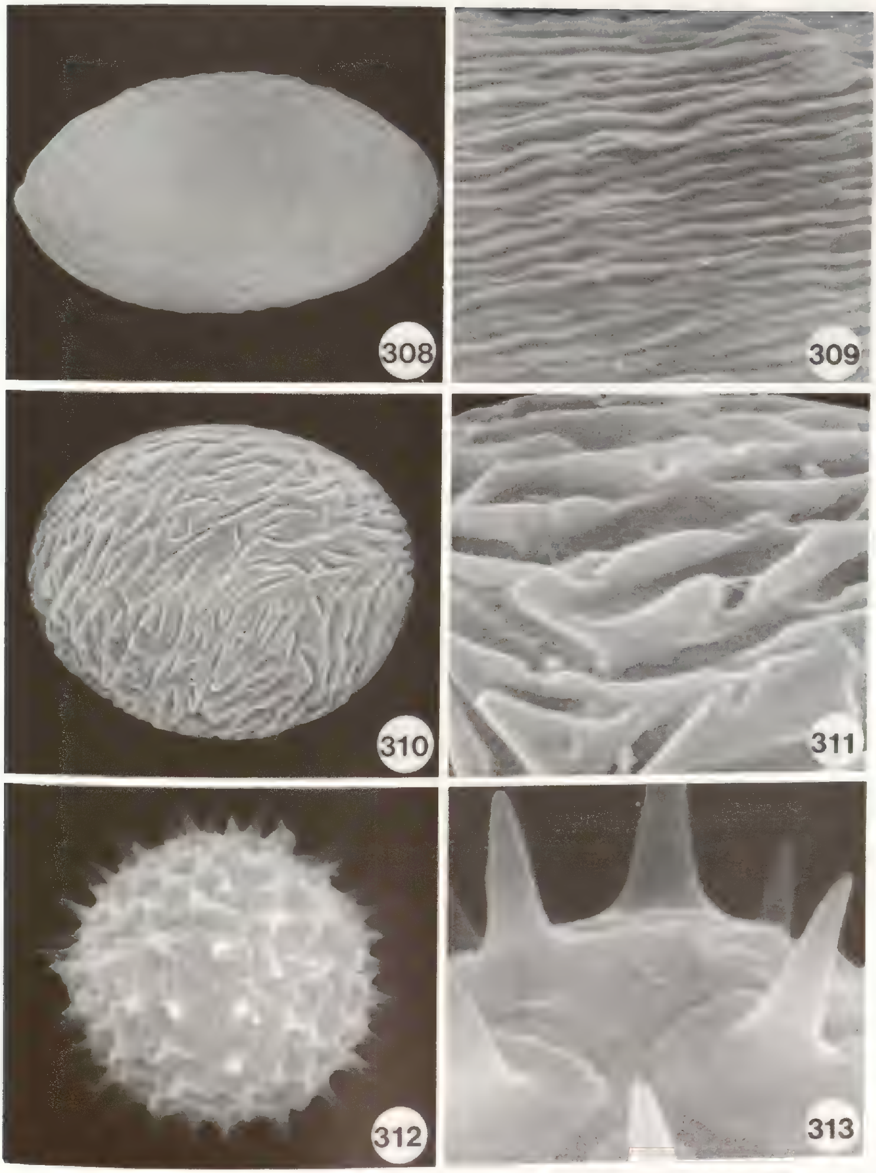
FIGURES 296–299. Pollen of *Syngonium* (species with spinose exine). 296, 297. *S. auritum* (P-3714). Fig. 296, ×1,970. 298, 299. *S. angustatum* (P-3713). Fig. 298, ×1,470.



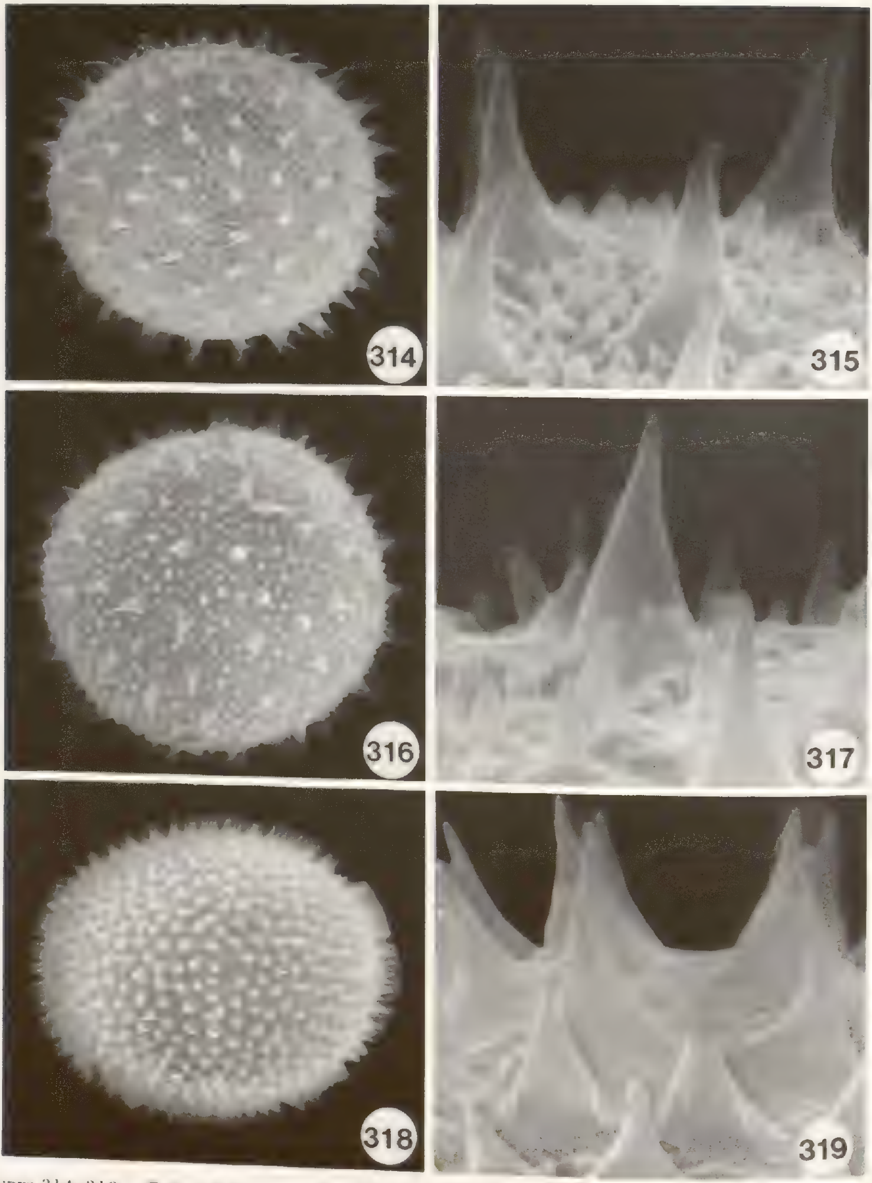
FIGURES 300–303. Pollen of *Syngonium* (species with tuberculate exine). 300–303. *S. standleyanum* (PS-366). Fig. 300, ×1,370. Fig. 301 shows the exine surface between the tubercles; Fig. 302 (×5,100) is a close-up of a single tubercle, and Fig. 303 shows the exine surface of the tubercle itself (cf. Figs. 216–219).



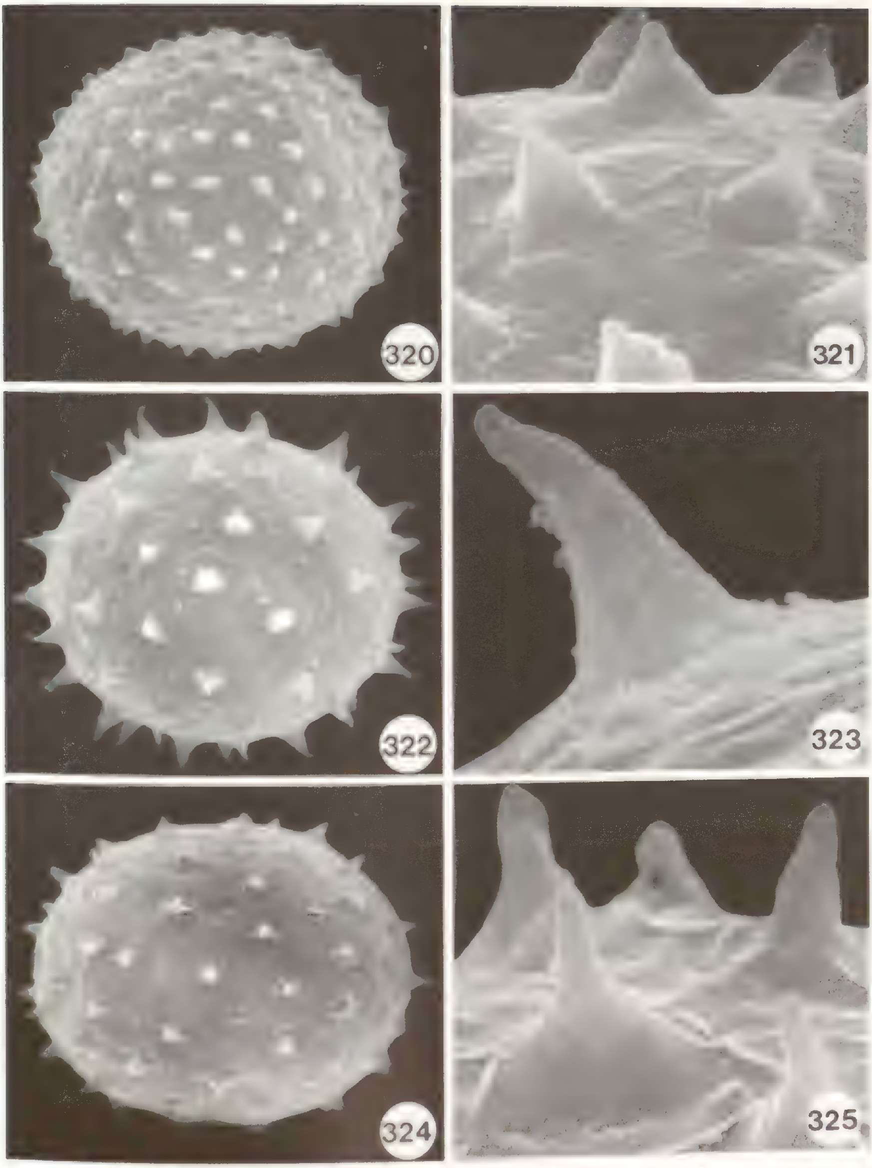
FIGURES 304–307. Pollen of *Steudnera*. 304–307. *S. discolor* (PS-199). Fig. 304 (×2,980) is a side view; Fig. 305 (×3,380) and Fig. 306 (×3,060) are views of the converging and nonconverging ends, respectively. See pollen description for explanation.



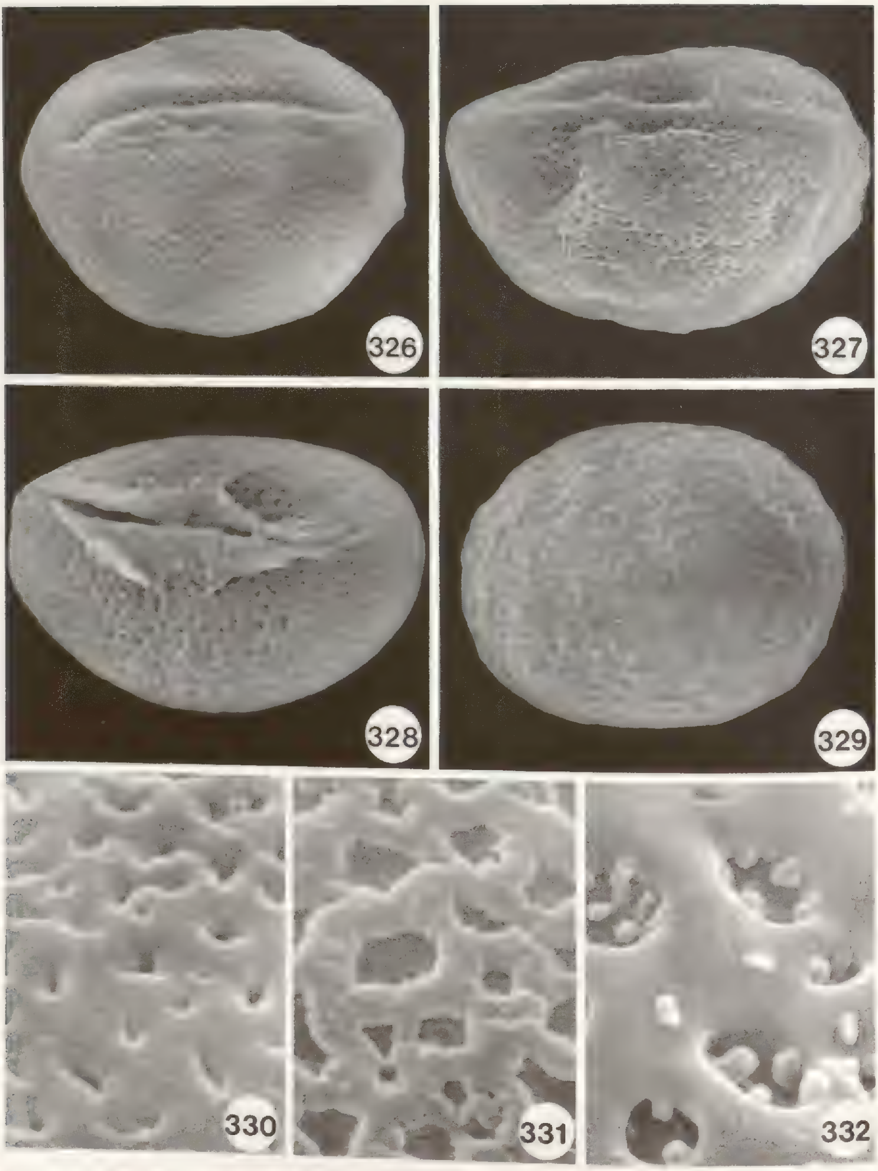
Figures 308–313. Pollen of *Colocasia*. 308, 309. *C. fallax* (PS-136). Fig. 308, ×3,310. 310, 311. *C. indica* (PS-160). Fig. 310, ×2,810. 312, 313. *C. esculenta* (PS-14). Fig. 312, ×2,625.



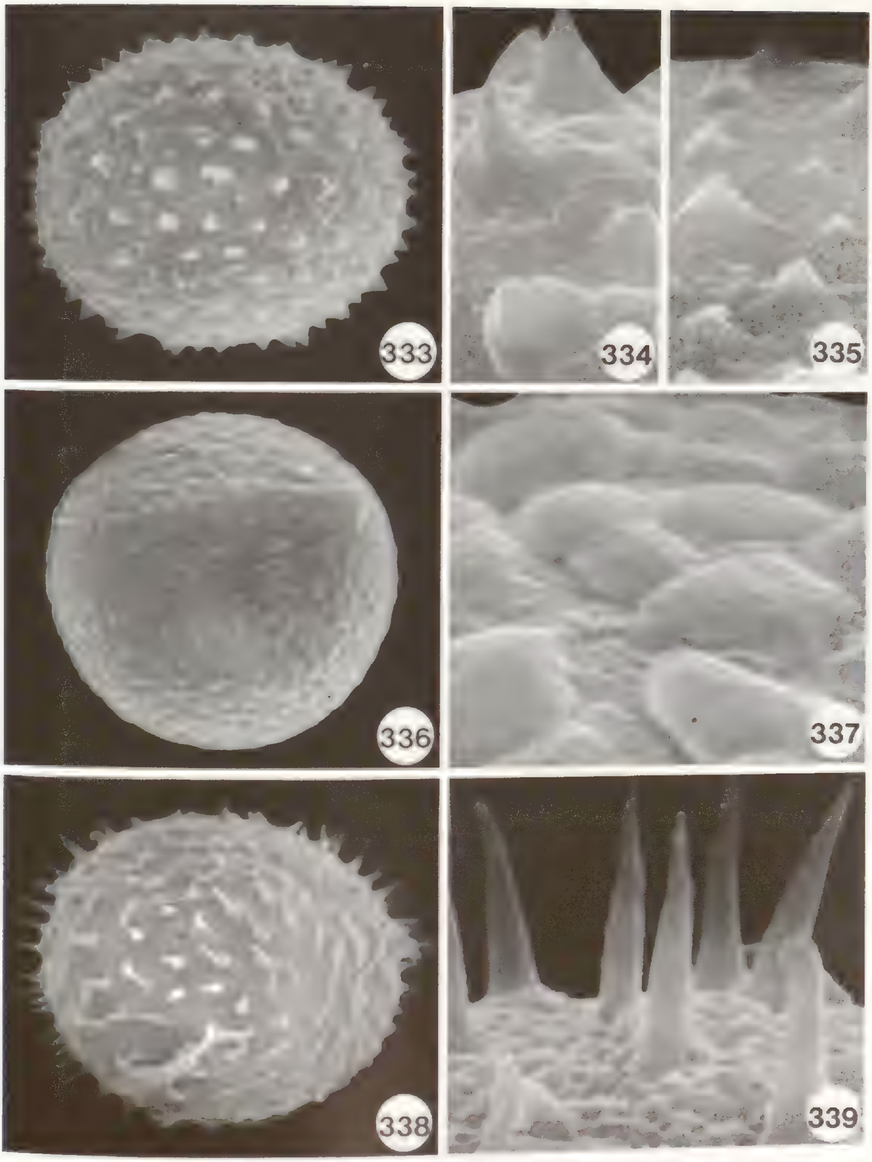
FIGURES 314–319. Pollen of *Gonatanthus* (314, 315), *Remusatia* (316, 317), and *Hapaline* (318, 319). 314, 315. *G. sarmentosus* (P-3696). Fig. 314, ×1,940. 316, 317. *R. vivipara* (P-3562). Fig. 316, ×1,900. 318, 319. *H. brownii* (PS-137). Fig. 318, ×1,590.



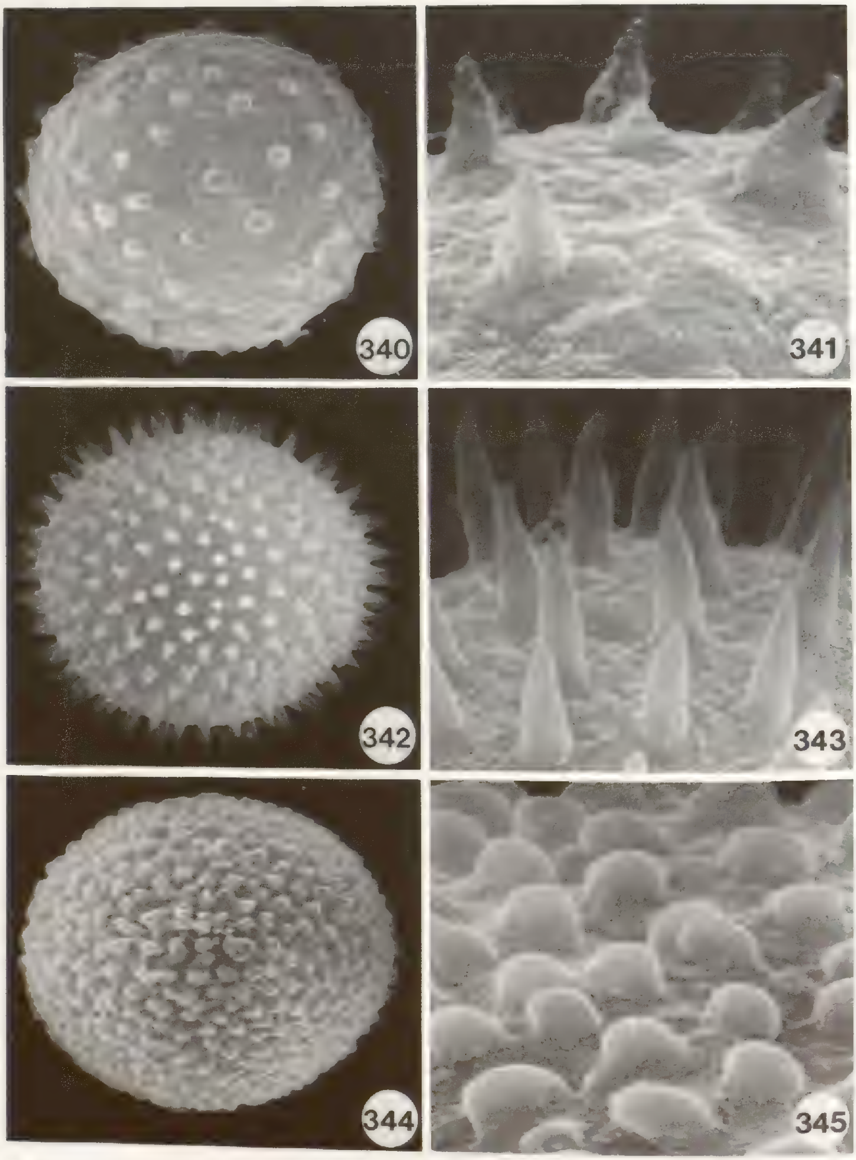
FIGURES 320–325. Pollen of *Alocasia*. 320, 321. *A. cucullata* (PS-460). Fig. 320, ×2,035. 322, 323. *A. portei* (PS-373). Fig. 322, ×1,420. 324, 325. *A. lauterbachiana* (P-3704). Fig. 324, ×1,790.



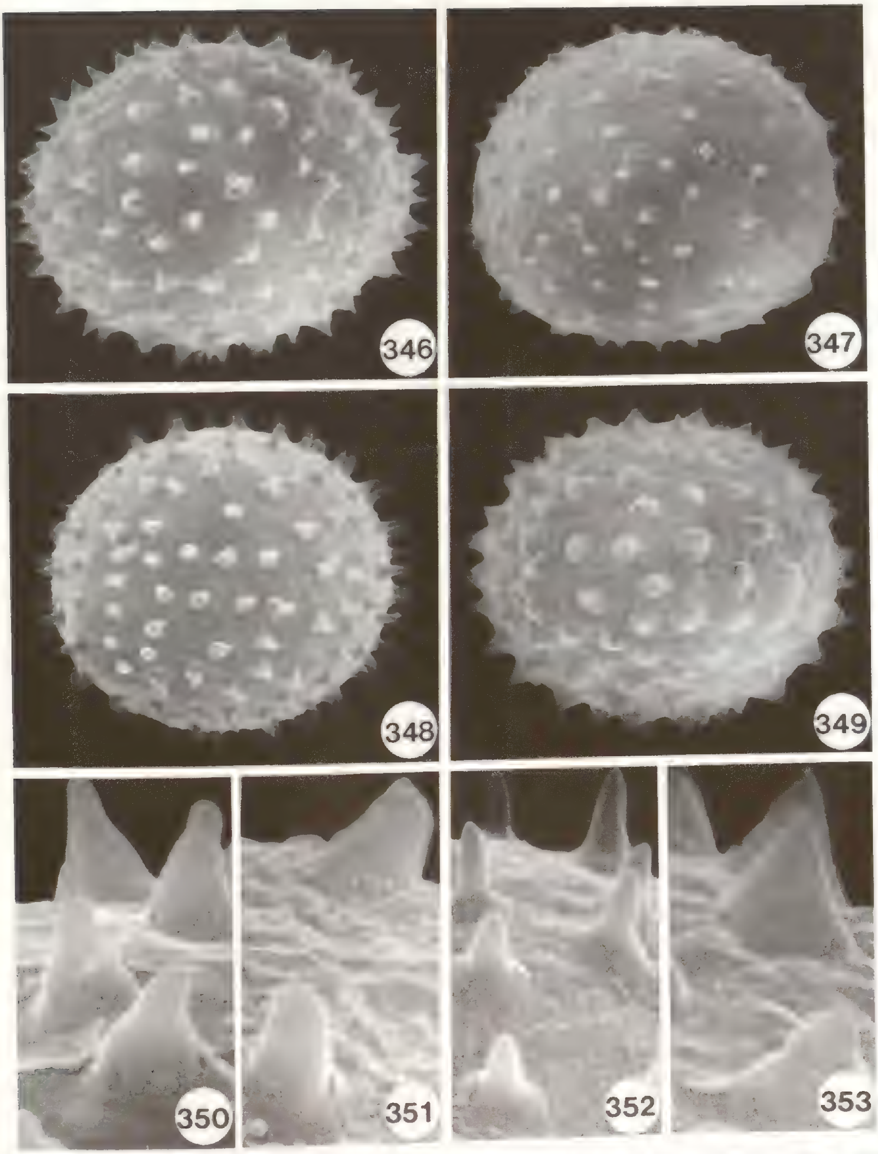
FIGURES 326–332. Pollen of *Stylochaeton*. 326, 327, 331. *S. natalensis* (P-3717). Fig. 326 (×1,130) shows the "apertural" (presumably distal) face, Fig. 327 (×1,370) the "nonapertural" (presumably proximal) face. 328, 330. *S. bogneri* (PS-243). Fig. 328, ×1,550. 329, 332. *S. zenkeri* (PS-244). Fig. 239, ×1,360.



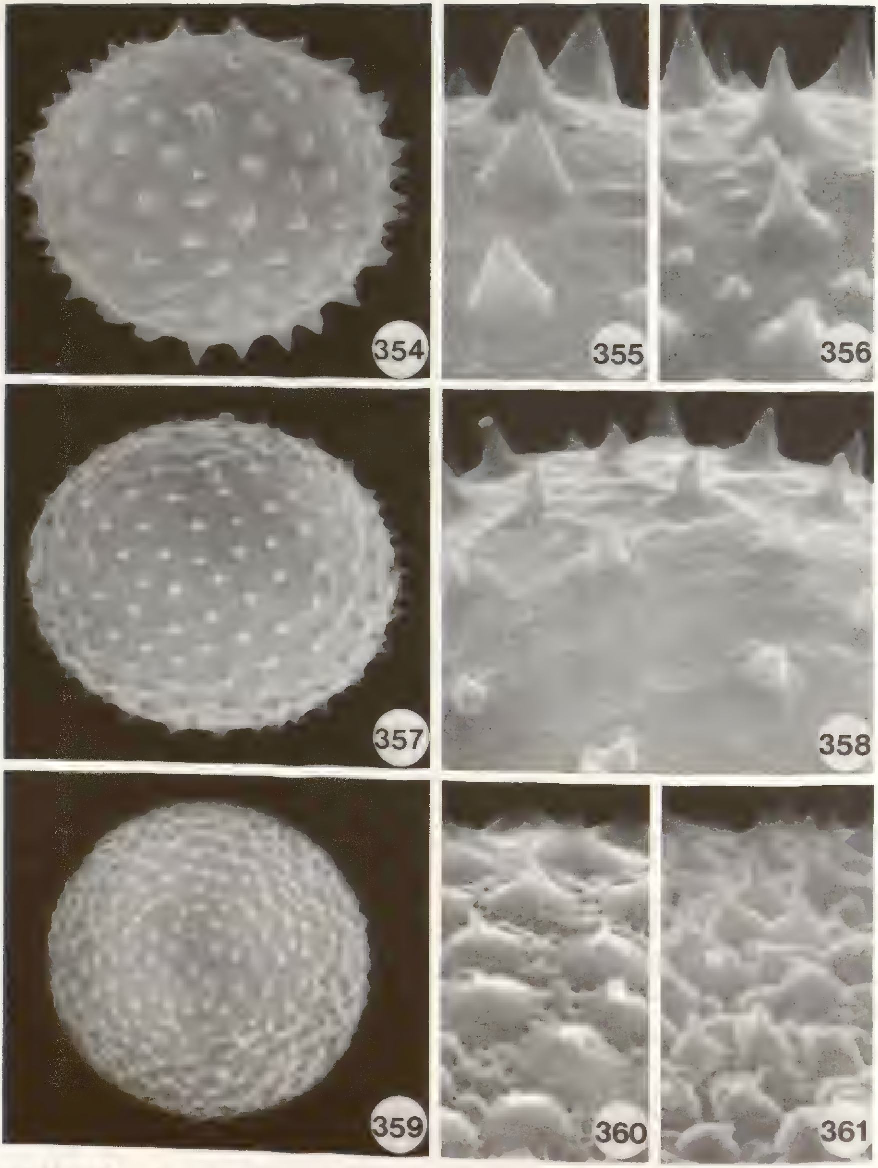
FIGURES 333–339. Pollen of *Arum* (333–335), *Dracunculus* (336, 337), and *Theriophonum* (338, 339). 333, 334. *A. dioscoridis* (P-3735). Fig. 333, ×2,240. 335. *A. maculatum* (PS-11). 336, 337. *D. vulgaris* (PS-510). Fig. 336, ×1,400. 338, 339. *T. infaustum* (PS-417). Fig. 338, ×1,990.



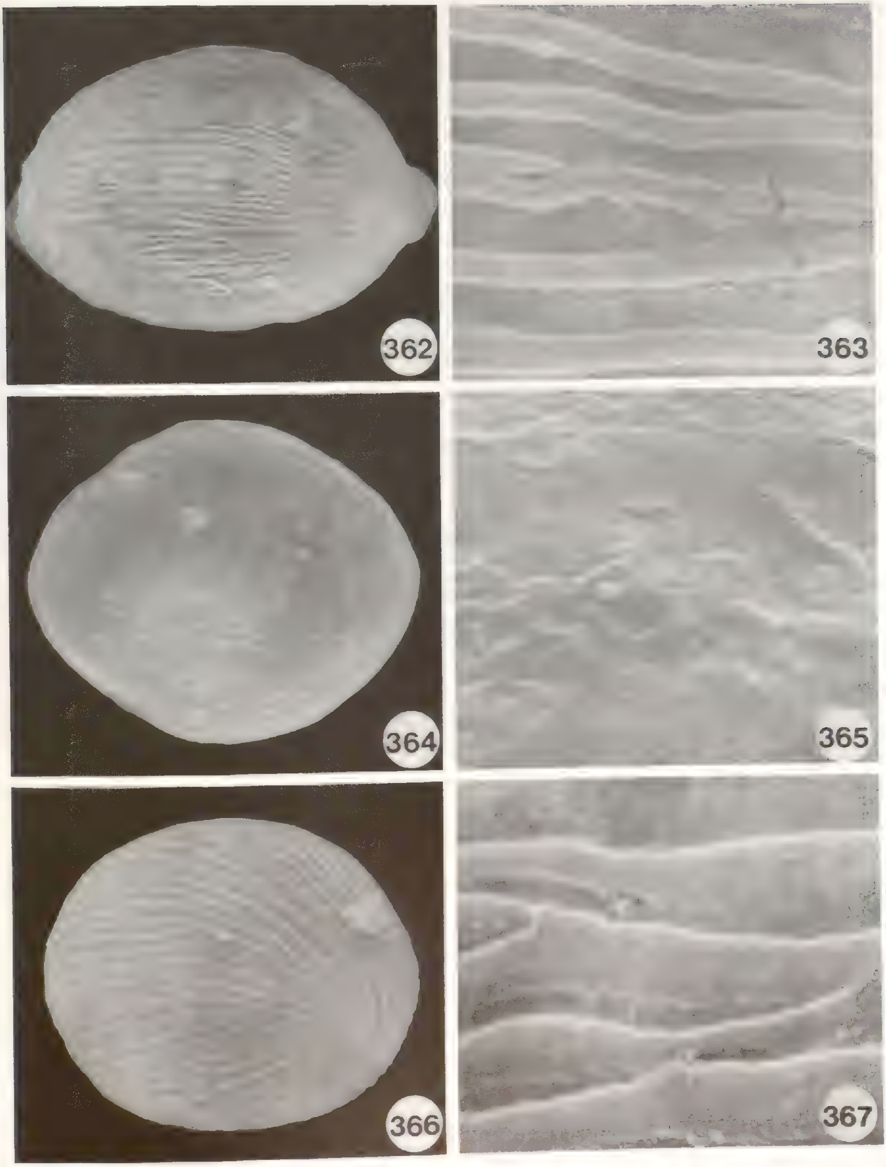
FIGURES 340–345. Pollen of *Typhonium*. 340, 341. *T. giraldii* (PS-419). Fig. 340, ×2,660. 342, 343. *T. blumei* (PS-380). Fig. 342, ×2,490. 344, 345. *T. trilobatum* (PS-324). Fig. 344, ×2,060.



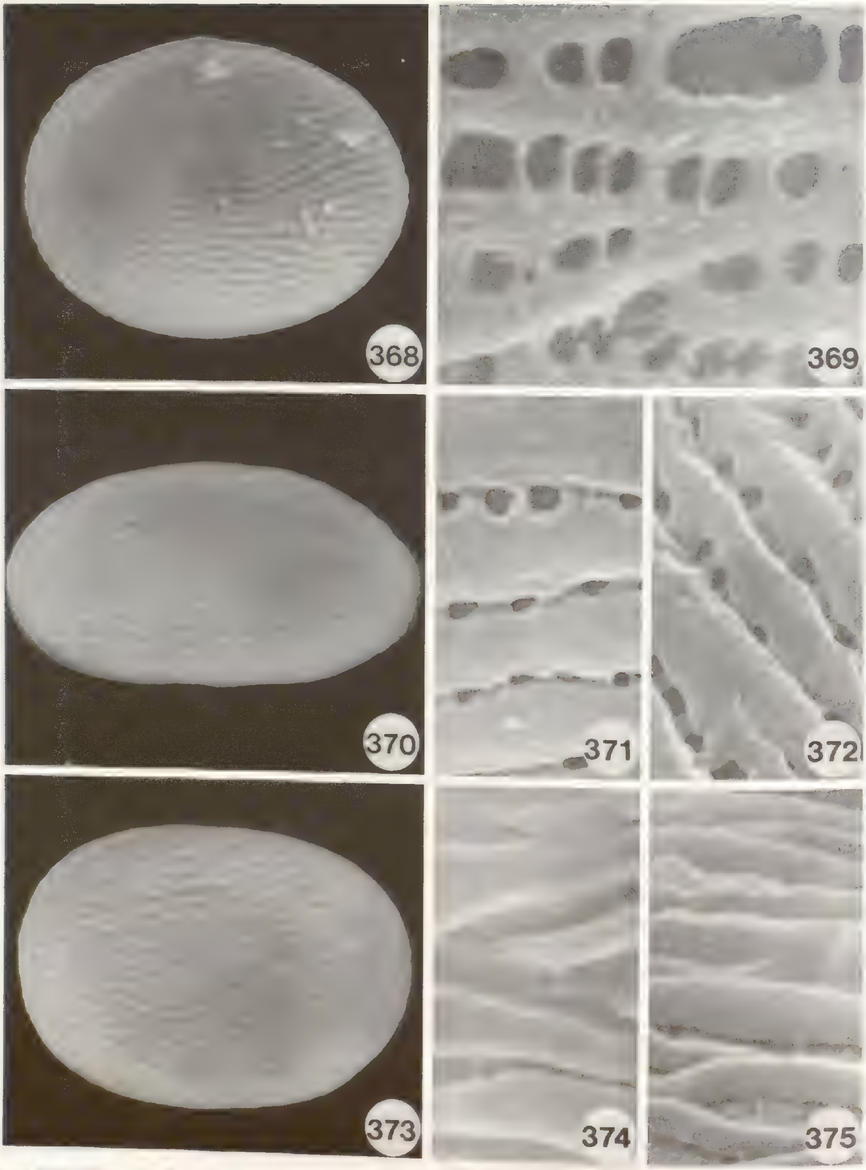
FIGURES 346–353. Pollen of *Sauromatum* (346, 350), *Eminium* (347, 351), and *Biarum* (348, 349, 352, 353). 346, 350. *S. venosum* (PS-241). Fig. 346, ×2,340. 347, 351. *E. intortum* (P-3573). Fig. 347, ×1,620. 348, 352. *B. spruneri* (PS-404). Fig. 348, ×3,180. 349, 353. *B. tenuifolium* (PS-326). Fig. 349, ×2,430.



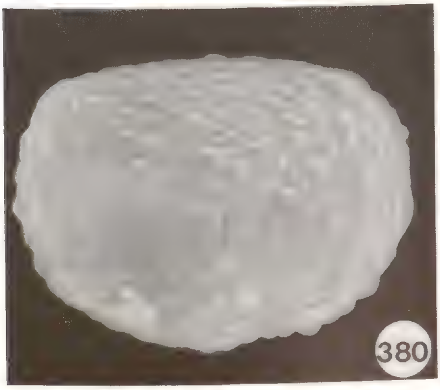
FIGURES 354–361. Pollen of *Arisaema* (354–356), *Ariopsis* (357, 358), and *Pinellia* (359–361). 354, 355. *Arisaema lichiangense* (P-3792). Fig. 354, ×2,750. 356. *Arisaema tortuosum* (P-3794). 357, 358. *Ariopsis peltata* (PS-235). Fig. 357, ×4,360. 359, 360. *P. cordata* (PS-97). Fig. 359, ×2,660. 361. *P. angustata* (P-3746).



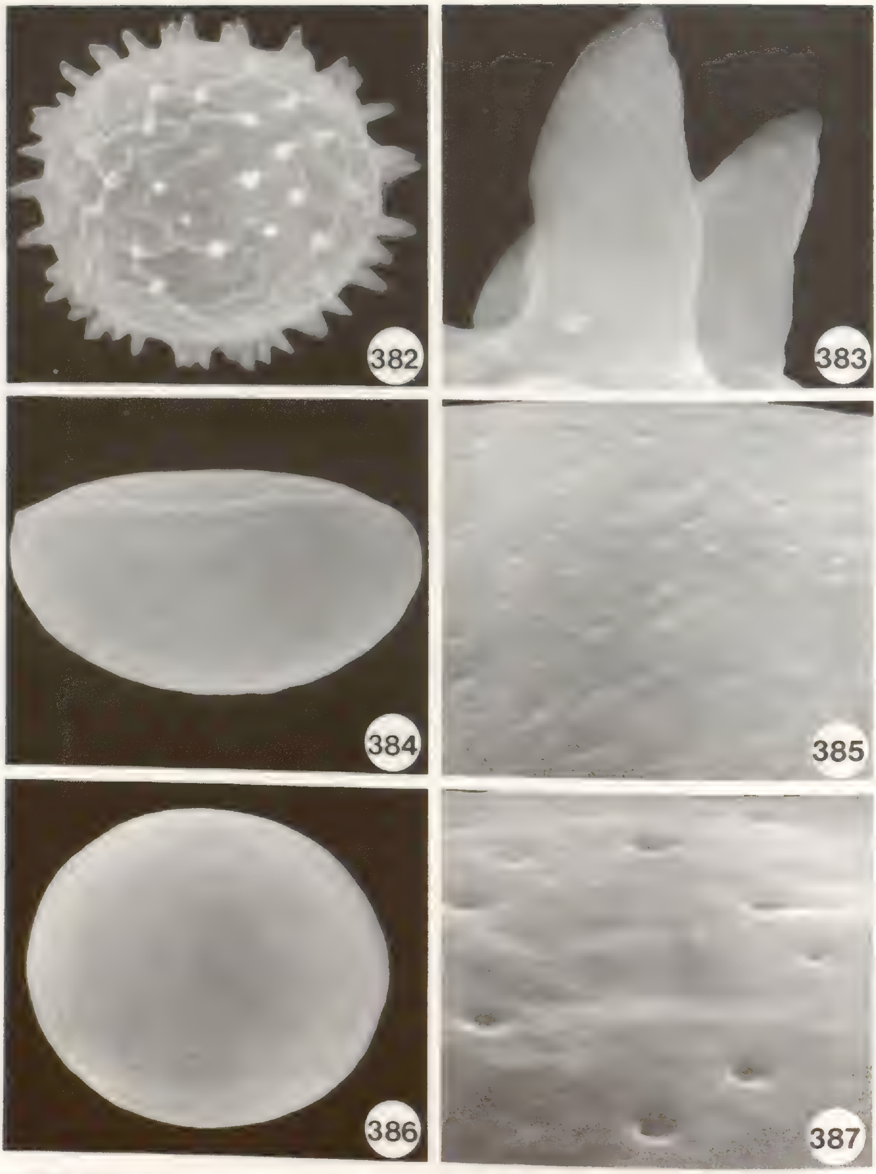
FIGURES 362–367. Pollen of *Pseudodracontium* (362, 363) and *Amorphophallus* (species previously segregated in *Plesmonium* and *Thomsonia*; 364–367). 362, 363. *P. siamense* (PS-413). Fig. 362, ×1,335. 364, 365. *A. margaritifer* (PS-411). Fig. 364, ×1,000. 366, 367. *A. sumawongii* (P-3551). Fig. 366, ×1,745.



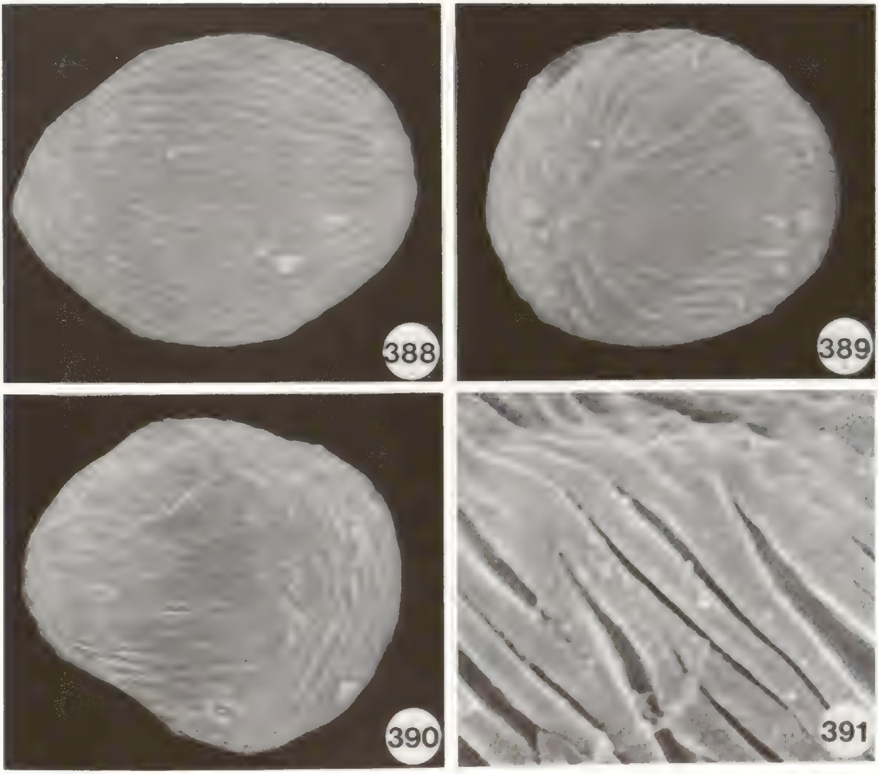
FIGURES 368–375. Pollen of *Amorphophallus* (species with striate-reticulate to striate exine). 368, 369. *A. putii* (PS-279). Fig. 368, ×1,430. 370–372. *A. longituberosus* (P-3635). Fig. 370, ×1,410. Fig. 371 shows the striae from a frontal view, Fig. 372 from an oblique view. 373–375. *A. kerrii* (PS-422). Fig. 373, ×1,230. Fig. 374 shows the striae from a frontal view, Fig. 375 from an oblique view.



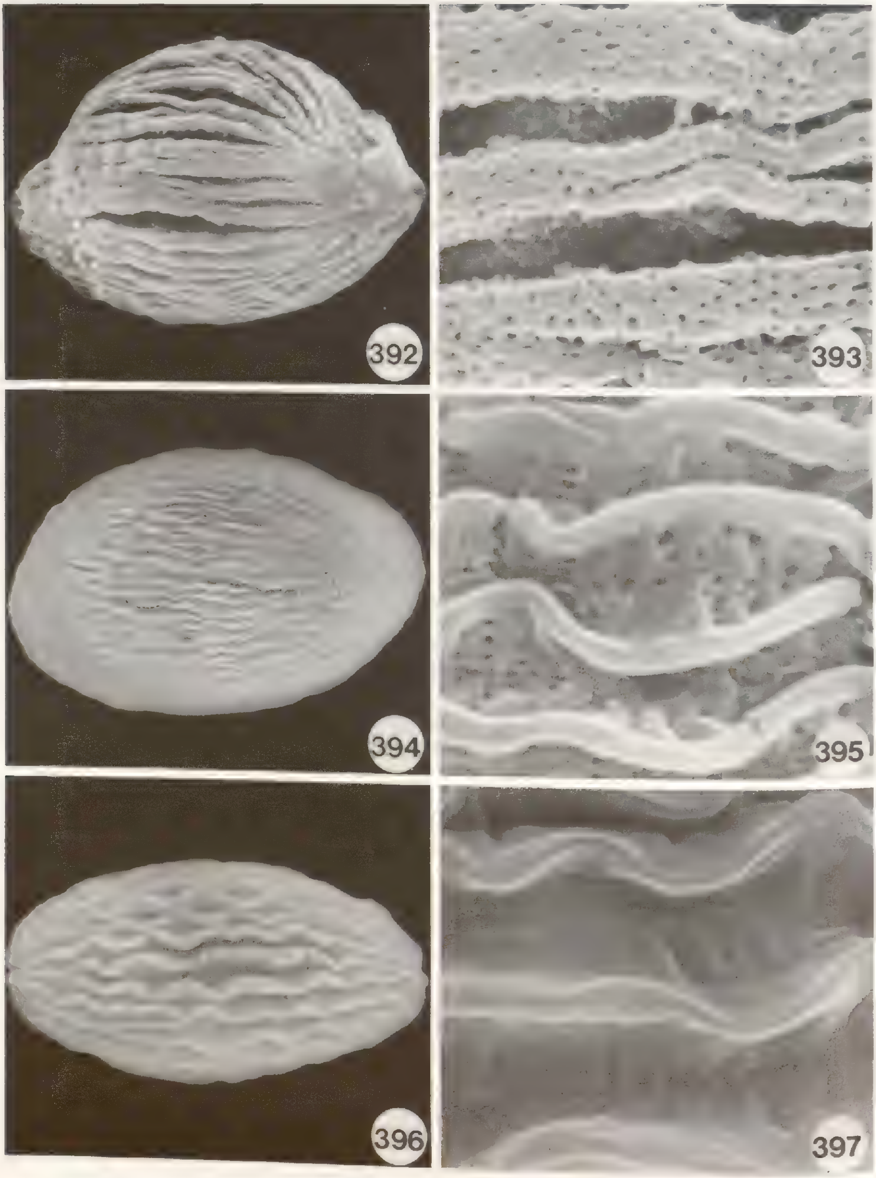
FIGURES 376–381. Pollen of *Amorphophallus* (species with striate to verrucate exine). 376, 377. *A. corrugatus* (PS-126). Fig. 376, ×1,400. 378, 379. *A. konjac* (PS-15). Fig. 378, ×1,800. 380, 381. *A. schweinfurthii* (P-3644). Fig. 380, ×1,230.



FIGURES 382–387. Pollen of *Amorphophallus* (species with spinose or subpsilate exine). 382, 383. *A. flavovirens* (PS-270). Fig. 382. ×1,350. 384, 385. *A. bulbifer* (PS-278). Fig. 384, ×1,535. 386, 387. *A. titanum* (PS-99). Fig. 386, ×850.



FIGURES 388–391. Pollen of *Protarum*. 388–391. *P. sechellarum* (PS-449). Fig. 388 (×2,680) is a side view. Fig. 389 (×2,680) and Fig. 390 (×2,600) are views of the converging and nonconverging ends, respectively (see pollen description for further explanation). 391. *P. sechellarum* (PS-412).



FIGURES 392–397. Pollen of *Arisarum* (392, 393), *Ambrosina* (394, 395), and *Pistia* (396, 397). 392, 393. *Arisarum vulgare* (PS-10). Fig. 392, ×2,310. 394, 395. *Ambrosina bassii* (PS-118). Fig. 394, ×1,615. 396, 397. *P. stratiotes* (PS-98). Fig. 396, ×2,470.

This wealth of available fossil pollen material (which we owe to the extraordinarily resistant property of sporopollenin) is perhaps the single most important reason that pollen morphology has come to be regarded as an especially critical source of taxonomic characters. Even when fossil pollen cannot be identified beyond the class level, it is still possible to study trends in character evolution over time and to assign polarities to character states of major pollen characters with confidence not often possible with other characters.

The fossil record has led most major contemporary workers (Muller, 1970; Doyle, 1973; Walker & Doyle, 1975; Zavada, 1983, and others) to the conclusion that monosulcate pollen is primitive for monocots as well as angiosperms as a whole. All monocot subclasses have at least one family with largely or exclusively monosulcate pollen, generally regarded as representing the primitive condition (Walker & Doyle, 1975; Zavada, 1983). Monosulcate pollen has been considered the most primitive type in palms (Sowunmi, 1968; Thanikaimoni, 1970; Harley, 1990), Cyclanthaceae (Harling, 1958), and the Alismatales (Chanda et al., 1988). Argue (1976) and Simpson (1987) considered pollen of Alismataceae and Pontederiaceae, respectively, to be ultimately monosulcate-derived, even though monosulcate pollen does not occur in these families. For Araceae, Erdtman (1952) conjectured that "it seems likely that the genera with monosulcate . . . pollen (*Pothos*, *Lysichiton*, etc.) are more 'primitive' than, for example, those with nonaperturate pollen grains. . . ." This hypothesis is amply borne out by the distribution of monosulcate pollen among the various aroid genera; as one would anticipate, it occurs almost exclusively in taxa with the most primitive floral plan—i.e., bisexual, perigoniate flowers. (The perigonium has been lost in *Pycnospatha*, but that genus is otherwise a member in good standing of the tribe Lasieae.)

Thus, monosulcate pollen is clearly to be regarded as primitive for Araceae, and all other types of aperturate as well as inaperturate pollen to be derived therefrom. The proposed scheme for the evolution of aperture types in Araceae is portrayed in Figure 489.

Pollen of *Acorus calamus* (Fig. 398) would perhaps be unique in Araceae in possessing a somewhat rounded, subulcerate aperture as opposed to an elongate sulcus. This is interpreted as a derived condition in this species, the aperture of *A. gramineus* being typically monosulcate. Since *Acorus* is very probably not an aroid at all (Grayum, 1987, 1991), the evolution of pollen characters in this genus will not be further discussed.

Zonate pollen probably was derived from monosulcate pollen via a circumferential extension of the sulcus, with the opposite ends meeting and merging to yield a continuous annular aperture. This model is bolstered by the existence of putative intermediate forms, i.e., pollen with "extended monosulcate" apertures (e.g., Fig. 404). The latter have been observed only in taxa in which fully zonate pollen is also known to occur—e.g., the Zamioculcadeae (Figs. 14, 16) and the Monstereae (Figs. 79, 80). It is impossible to be certain whether any species is characterized solely by extended monosulcate pollen, but it is at least very frequent in *Zamioculcas zamiifolia* and *Rhaphidophora reineckei*. In *Gonatopus angustus* (Figs. 15–17), fully zonate and extended monosulcate grains are produced by the same plant, and presumably even in the same anther locule.

Sowunmi (1968) and Thanikaimoni (1970) agreed that zonate pollen in palms is derived from monosulcate pollen via the intermediate extended monosulcate condition, and a similar transformational sequence has been postulated for the lilialean families Heloniadaceae and Uvulariaceae (Roth et al., 1987). Muller (1970) indicated that the trend from monosulcate to zonate pollen is standard for monocots as a whole; however, Zavada (1983) did not comment on this issue. Walker & Doyle (1975) proposed the same pathway for magnoliid dicots.

Within the zonate category, two further specializations may be mentioned. In certain species of *Stenospermation*, the extra-apertural halves of the exine become highly reduced and are dwarfed by the bulging aperture membrane (Figs. 111, 112). Another tendency, observed in *Epipremnum pinnatum* (Figs. 101, 102) and particularly *Amydrium humile* (Figs. 95–98), is toward heteromorphy of the extra-apertural halves, both in terms of size and, most strikingly, exine sculpturing.

Species with zonate pollen occur together with diaperturate-grained species in two of the three aroid genera in which diaperturate pollen is known, *Heteropsis* and *Rhaphidophora* (the third genus, *Calla*, being monotypic). This is also the case in several other taxa outside the Araceae, for example, the palm genera *Salacca*, *Plectocomia*, and *Korthalsia* (Thanikaimoni, 1970); the family Rapateaceae (Zavada, 1983); and in *Nymphaea* of the dicot family Nymphaeaceae (Erdtman, 1952). It is hard to escape the conclusion that there is a close relationship between the two aperture types in Araceae. One might imagine two different pos-

TABLE 1. Summary of pollen morphology data.

	Description on page:	Aperture type	Pollen shape	Mean pollen size (μm)	Exine sculpturing
I. Subfamily Pothoideae Engl.					
Gymnostachys	9	M	boat-shaped	31	foveolate
Pothos	9	M	boat-shaped	21	foveolate to reticulate
Pedicellarum	9	M	boat-shaped	*18	reticulate
Pothoidium	10	M	boat-shaped	26	reticulate
Zamioculcas	10	Zx	hamburger-shaped	60	fossulate-foveolate
Gonatopus	10	Z(x)	hamburger-shaped	76	foveolate
Anadendrum	10	I	globose	22	spinulose-pilate
Anthurium	11	F(I)	globose	22	spinulose-reticulate to spinose or gemmate
Spathiphyllum	12	I	boat-shaped	32	striate
Holochlamys	13	I	boat-shaped	33	striate (BB)
Heteropsis	13	Z, D	hamburger- or boat-shaped	40	foveolate
Rhaphidophora	13	Z(x), D	hamburger- or boat-shaped	33	foveolate, rugulate, verrucate, psilate, etc.
Monstera	14	Z	hamburger-shaped	48	foveolate
Amydrium	14	Z	hamburger-shaped	39	foveolate to punctate
Epipremnum	15	Z	hamburger-shaped	40	foveolate
Scindapsus	15	Z	hamburger-shaped	38	remotely punctate
Alloschemone	15	?	?	46	foveolate
Stenospermation	15	Z, I	hamburger- or boat-shaped	42	psilate to foveolate or verrucate
Rhodospatha	16	Z, I	hamburger- or boat-shaped	47	remotely punctate to verrucate
II. Subfamily Calloideae Schott					
Calla	17	D	globose	23	foveolate
Furtadoa	19	I	boat-shaped	17	psilate
Homalomena	19	I	boat-shaped	22	psilate to obscurely verruculate
Aglaonema	19	I	boat-shaped	*52	psilate
Aglaodorum	19	I	boat-shaped	59	(psilate)
Zantedeschia	20	I	boat-shaped	40	psilate
Anubias	20	I	globose	24	psilate to verrucate
Schismatoglottis	20	I	boat-shaped	20	psilate

TABLE 1. Continued.

	Description on page:	Aperture type	Pollen shape	Mean pollen size (μm)	Exine sculpturing
Piptospatha	21	I	boat-shaped	25	psilate
Bucephalandra	21	I	ellipsoid	*29	psilate
Phymatarum	21	I	boat-shaped	*19	psilate
Aridarum	21	I	boat-shaped	23	psilate
Heteroaridarum	21				
Hottarum	21	I	boat-shaped	*14	psilate
Typhonodorum	21	I	boat-shaped	45	verruculate and punctate
Peltandra	22	I	boat-shaped or globose	33	spinose or psilate
Philodendron	22	I	boat-shaped	40	psilate to verrucate
Dieffenbachia	23	I	boat-shaped to globose	79	psilate to foveolate or tuberculate
Bognera	23	I	boat-shaped	59	scabrate
Cryptocoryne	23	I	boat-shaped	34	psilate
Lagenandra	24	I	boat-shaped	36	psilate
Carlephyton	25	I	globose	34	spinose
Colletogyne	25	I	globose	39	spinose
Arophyton	25	I	globose	32	spinose
Mangonia	25	(I)	(boat-shaped)	(40)	(verrucate)
Asterostigma	25	I	boat-shaped	36	psilate to verrucate
Synandrospadix	26	I	globose	49	spinose
Taccarum	26	I	boat-shaped	63	scabrate to spinose
Gorgonidium	26	I	boat-shaped	34	retiverrucate to verrucate
Gearum	26	I (Mx?)	ellipsoid	*56	psilate or ±verrucate
Spathantheum	26	I	boat-shaped	54	psilate
Spathicarpa	27	I	boat-shaped	48	psilate
Culcasia	10	I	globose	32	subreticulate to verrucate or spinose
Cercestis	27	I	boat-shaped	*39	fossulate
Nephthytis	27	I	boat-shaped	*46	verrucate
Anchomanes	28	I	boat-shaped	64	psilate or scabrate
Pseudohydrosme	28	I	boat-shaped	*106	psilate
Montrichardia	28	I	globose	94	psilate
Callopsis	28	I	globose	37	papillate

TABLE 1. Continued.

	Description on page:	Aperture type	Pollen shape	Mean pollen size (μm)	Exine sculpturing
III. Subfamily Colocasioideae Engl.					
Filarum	24	I	globose	*21	spinose
Ulearum	24	I	globose	26	spinose
Zomicarpella	24	I	globose	*19	spinose
Zomicarpa	24	I	globose	32	spinose
Jasarum	29	I	boat-shaped	44	reticulate
Scaphispatha	29	I	globose	45	verrucate
Caladium	29	I	globose	41	psilate
Xanthosoma	29	I*	boat-shaped or globose	42	punctate or verruculate
Chlorospatha	30	I*	globose	26	psilate or reticulate
Syngonium	30	I	boat-shaped to globose	48	nearly psilate to verrucate, rugulate, spinose or tuberculate
Protarum	38	I	boat-shaped	*21	striate (BB)
Steudnera	30	I	boat-shaped	22	striate (BB)
Colocasia	31	I	boat-shaped to globose	25	striate to spinose
Gonatanthus	31	I	globose	32	spinose
Remusatia	31	I	globose	33	spinose
Hapaline	31	I	globose	40	spinose
Alocasia	31	I	globose	35	spinose
IV. Subfamily Lasioideae Engl.					
Orontium	16	M	boat-shaped-elongate	64	foveolate
Lysichiton	16	M	boat-shaped	40	reticulate
Symplocarpus	16	M	boat-shaped	33	reticulate
Cyrtosperma	17	M	boat-shaped	28	foveolate to reticulate
Lasimorpha	17	M	boat-shaped-elliptic	22	foveolate or subreticulate
Anaphyllopsis	17	M	boat-shaped-elliptic	31	foveolate
Lasia	17	M	boat-shaped	27	reticulate
Anaphyllum	18	M	boat-shaped	29	foveolate to reticulate
Podolasia	18	M	boat-shaped	18	verruculate
Urospatha	18	M	boat-shaped	26	reticulate
Dracontioides	18	M	boat-shaped	23	reticulate
Dracontium	18	M	boat-shaped	36	foveolate to reticulate
Pycnospatha	18	M	boat-shaped	34	reticulate
Stylochaeton	32	MxI	boat-shaped	53	reticulate

Table 1. Continued.

	Description on page:	Aperture type	Pollen shape	Mean pollen size (μm)	Exine sculpturing
V. Subfamily Aroideae Engl.					
Arum	32	I	globose	32	spinose
Dracunculus	33	I	boat-shaped or globose	45	verrucate
Helicodiceros	33	(I)	(globose)		(spinose)
Theriophonum	33	I	globose	*25	spinose-reticulate
Lazarum	33	I	ellipsoid	*37	spinose
Typhonium	33	I	globose	32	spinose to verrucate
Sauromatum	34	I	globose	33	spinose
Eminium	34	I	globose	44	spinose
Biarum	34	I	globose	30	spinose
Arisaema	34	I	globose	22	spinose
Ariopsis	35	I	globose	20	spinulose
Pinellia	36	I	globose	25	spinulose-reticulate to spinulose
Pseudodracontium	36	I	boat-shaped	48	striate
Amorphophallus	36	I	boat-shaped to globose	53	striate-reticulate to striate, psilate, spinose or verrucate
Arisarum	38	I	boat-shaped-elongate	45	striate-foveolate
Ambrosina	38	I	boat-shaped	44	striate-reticulate
Pistia	38	I	boat-shaped	27	plicate

KEY:

Aperture Type:
D—diaperturate
F—forate
I—inaperturate
M—monosulcate
Z—zonate
Mx—monosulcoidate
Zx—extended monosulcate
*—pollen in permanent tetrads (size given of individual grains)

Mean Pollen Size:
*—measured from SEM micrographs

Exine Sculpturing:
(BB)—striations in "baseball" pattern (see discussion under *Holochlamys*); where not indicated, striations are in the "football" pattern

( )—data from literature (see pollen descriptions for sources)

This table indicates only the basic conditions and most common variations. See pollen descriptions for further information.

sibilities: either diaperturate pollen has been derived from zonate pollen via the closure of the aperture at two opposite loci; or, alternatively, zonate and diaperturate pollen have both been derived independently from extended monosulcate pollen, the former via a breach of the gap separating the ends of the sulcus, the latter via a closure of the aperture at a single locus. Although neither of these two possibilities appears farfetched, the second is perhaps the more parsimonious in that it presupposes only a single closure of the aperture rather than two. It is also of interest that in the palm genera *Plectocomia* and *Korthalsia*, species with extended monosulcate pollen are known in addition to those having diaperturate or zonate pollen (Thanikaimoni, 1970). In these cases it is more parsimonious to envision the existence of two rather than three successive "generations" of a transformational sequence within a single genus.

For palms, Sowunmi (1968) preferred the pathway to diaperturate pollen departing from the extended monosulcate, rather than the zonate, condition. Indeed, the portion in question of her evolutionary scheme for aperture types strikingly resembles the one presented here for Araceae, including placement of the question mark. Figure 489 of the present work was completed and photographed long before I saw Sowunmi's paper. Thanikaimoni (1970) was even more emphatic in his preference for the extended monosulcate-diaperturate pathway in palms, omitting the question mark and stating that he observed no tendency for any zonate-diaperturate transformation. Muller (1970), on the other hand, suggested that zonate pollen is antecedent to diaperturate pollen for monocots as a whole. In the magnoliid dicots, diaperturate pollen is believed to have been derived secondarily from inaperturate pollen (Walker & Doyle, 1975).

The forate pollen of *Anthurium* is harder to explain. Erdtman (1952) correctly observed that "*Anthurium* is isolated both pollen-morphologically and systematically." Forate pollen is common in other monocot families, notably Alismataceae (Figs. 581, 583), Costaceae (Punt, 1968), Cyperaceae (Erdtman, 1952), and Bromeliaceae (Ehler & Schill, 1973). Fischer (1890), however, segregated the various forate types into two categories: (1) the apertures in Alismataceae, Cyperaceae, and Bromeliaceae as well as in the nonforate, aperturate Araceae investigated (*Acorus, Calla*) were held to represent merely thin parts of the exine ("Austrittstellen," or "exit-places"); (2) apertures in *Anthurium* and Costaceae as well as the solitary pores in *Pandanus* were considered actual holes ("Keimporen," or "germinal pores"). Thus the forate so-called apertures in *Anthurium* may not be homologous with other aroid apertures. TEM studies will be required to settle this issue.

Argue (1976) asserted that the forate pollen of Alismataceae is "almost certainly" derived from monosulcate ancestors, possibly via inaperturate intermediates. Zavada (1983) derived forate pollen directly from the monosulcate type for monocots in general. Forate pollen in the dicot subclass Magnoliidae is thought to have been derived directly from inaperturate ancestors (Walker & Doyle, 1975). Muller (1970) believed that forate pollen is generally derived from inaperturate pollen for monocots as a whole; he did specifically address the case of *Anthurium*, however, the pollen of which he believed to be derived directly from zonate ancestors. This belief was founded on Fischer's (1890) description of *Anthurium* pollen as having the pores all in a single plane. Actually, Fischer merely described the three or four pores (in the four species he examined) as being in a large circle, probably referring rather loosely to their distribution on the surface of the grain. Having observed thousands of pollen grains representing over 50 species in the genus under SEM, I can confidently state that the pores in *Anthurium* pollen are seldom, if ever, in a single plane (hence the choice of the term "forate"). They are usually scattered and quite irregularly arranged, as opposed to the evenly spaced, geometrical distribution of pores in the Alismataceae. Neither are they ever as numerous as in that family, though the precise number is generally difficult to determine.

The most logical and parsimonious scenario for the evolution of forate pollen grains in *Anthurium* would derive them directly from monosulcate predecessors. An inaperturate intermediate stage is conceivable, but there is no reason to postulate one. Section *Polyphyllium* of *Anthurium* does apparently possess inaperturate pollen (Fig. 29); however, it is otherwise of a very bizarre and highly specialized type more reasonably envisioned as derived from the typical forate condition. In terms of its floral and vegetative morphology and anatomy, *Anthurium* is obviously much more closely akin to Araceae possessing monosulcate pollen (Potheae, Lasieae, and others) than to the mainstream of inaperturate-grained taxa. Hence, even if the forate pollen of *Anthurium* were found to be inaperturate-derived, it would become necessary to postulate only that the inaperturate character state had been acquired independently from the rest of

Araceae; thus, the matter is of little consequence to the phylogeny of the genus.

Inaperturate pollen is virtually always derived from monosulcate pollen and may be considered the effective end of the evolutionary line. There is no reason to suspect that the trend from aperturate to inaperturate pollen has ever been reversed in Araceae. This is contrary to the situation for monocots as a whole, wherein forate pollen is envisioned to have been derived from inaperturate pollen (Muller, 1970), as well as for magnoliid dicots, in which inaperturate pollen has supposedly given rise secondarily to various multiaperturate types (Walker & Doyle, 1975).

There are only three araceous genera in which inaperturate pollen may have evolved from some type other than monosulcate pollen. In *Anthurium* sect. *Polyphyllium*, inaperturate pollen most likely evolved from the forate type typical of that genus. The remaining two genera—the closely related *Rhodospatha* and *Stenospermation*—are more problematic. Both genera contain species with zonate pollen in addition to species with inaperturate pollen, and some species of *Stenospermation* have the specialized zonate pollen with highly reduced extra-apertural exine halves. It is thus tempting to speculate that perhaps this so-called "inaperturate" pollen is actually omni-aperturate, i.e., that the extra-apertural exine has been nearly or completely lost. The pollen of *Stenospermation* sp. indet. (Fig. 417) would then be envisioned as having a small patch (or two) of extra-apertural exine (Fig. 117), with outlying verrucae (Fig. 118) representing the vestiges of its former extent (or, alternatively, verrucae of the expanded aperture membrane). The remaining three inaperturate species studied—*Stenospermation* sp. ined. (Fig. 114), *Rhodospatha pellucida* (Fig. 121), and *R. venosa*—might have lost their extra-apertural exine altogether. Such a hypothesis must of course be confirmed by TEM studies.

Alternatives to the foregoing scheme would require that the inaperturate pollen of these species be derived directly from typical zonate pollen (i.e., via a complete closure of the aperture) or, more logically, from monosulcate ancestors. But the latter alternative would entail the unattractive corollary that zonate pollen must have evolved independently in these genera. In any case, the discovery of inaperturate pollen in the tribe Monstereae makes the tribe Spathiphylleae look more at home in the subfamily Monsteroideae.

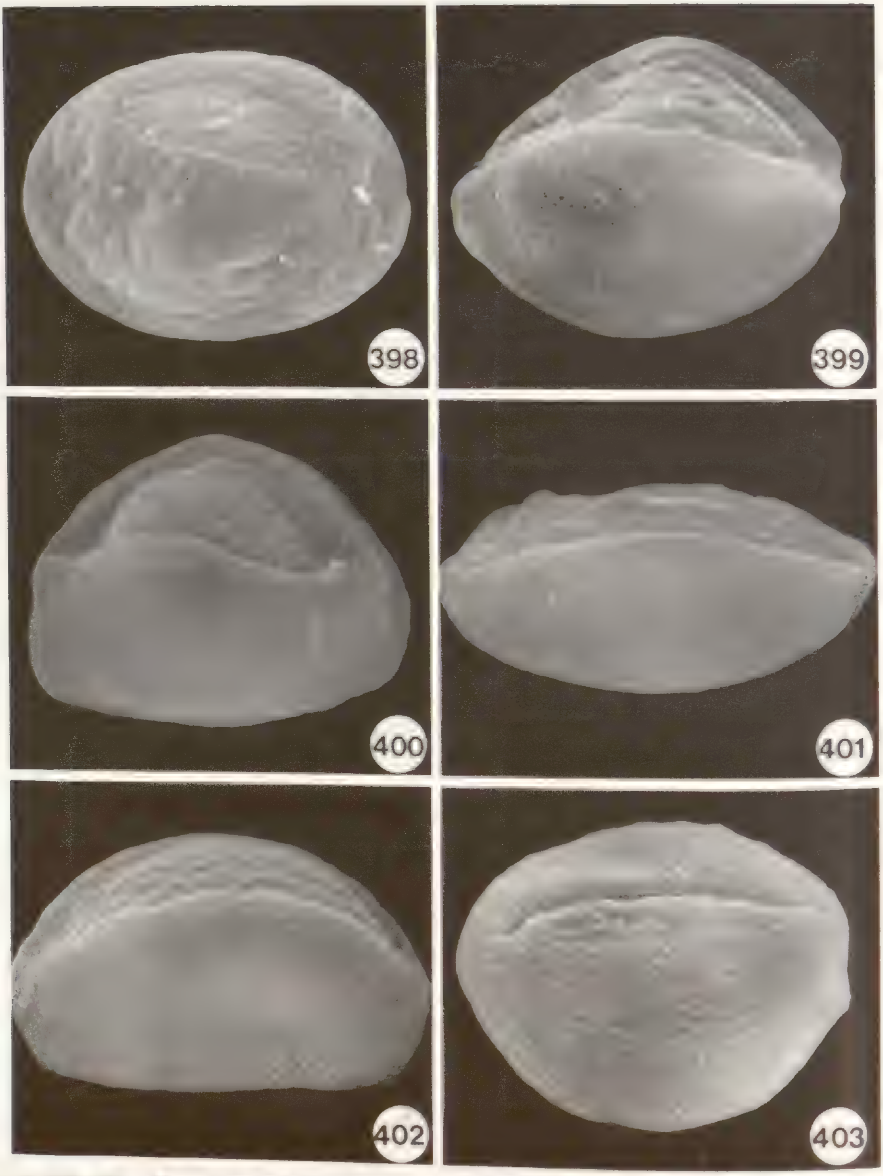
The evolution of inaperturate pollen from monosulcate pollen, which must have happened on numerous occasions in Araceae, must naturally have proceeded via a "monosulcoidate" state, comprising functionally inaperturate pollen with a distinct, elongate suture or seam representing the vestige of a sulcus. Although one would not expect to actually encounter such a transitional stage in any extant genus, it does occur in *Stylochaeton* sect. *Spirogyne* (Fig. 403). Taking the totality of floral, vegetative, and pollen characters into account, this genus appears to occupy a comparably transitional evolutionary grade. It combines perigoniate flowers, a primitive androecium and an apparent lack of "laticifers" with monoecy, an advanced spathe type and other advanced features. In other words, this is precisely where such a transitional pollen aperture type ought to turn up. That the transition from monosulcoidate (or even monosulcate) to inaperturate pollen may have already occurred within the genus *Stylochaeton* is suggested by the presence of apparently fully inaperturate pollen in the florally more specialized sect. *Stylochaeton* (Fig. 329).

Gorgonidium vargasii (Fig. 252) and *Gearum brasiliense,* in the likewise more or less transitional tribe Spathicarpeae, also appear to have monosulcoidate grains, but here the evidence is more tenuous and additional material needs to be examined, preferably at the TEM level.

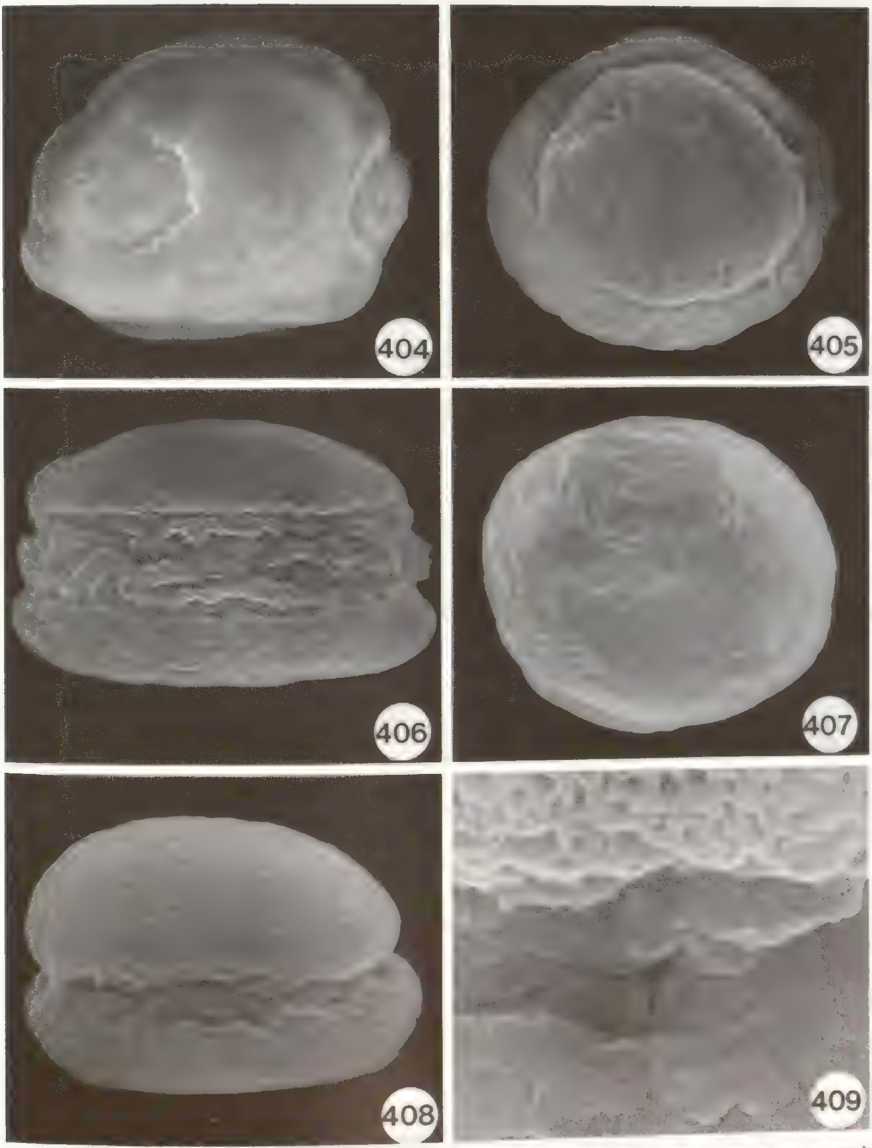
POLARITY, SHAPE, AND SYMMETRY

An understanding of the absolute polarity of pollen grains is critical to describing pollen shape, symmetry, and aperture type. Polarity must be studied while the microspores are still in the tetrad stage (Walker & Doyle, 1975). This has been accomplished among aroids, so far as I am aware, only for *Spathiphyllum wallisii.* Hence aperture types in Araceae have been described in general terms in this paper, and several key assumptions have had to be made in describing pollen shape and symmetry, as discussed below. Pollen shape is quite variable, depending upon environmental factors and the method of preparation for study. For the present study, shape was judged from a composite of light slides and all available SEM micrographs; the particular photograph chosen for publication may or may not be representative of the species in question in terms of shape, though every effort was made to make it so.

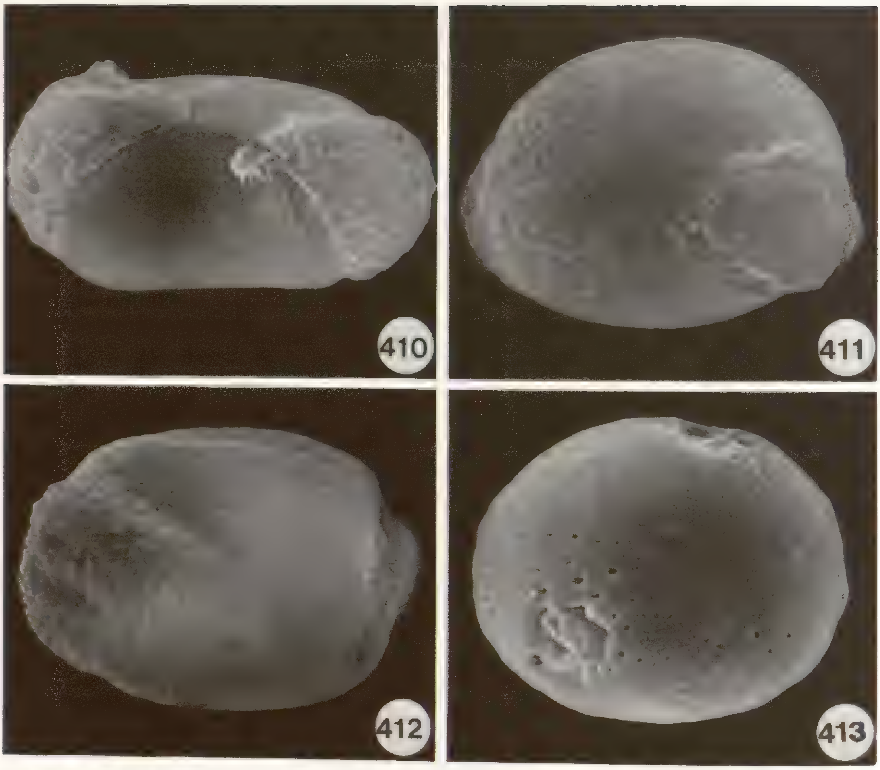
Monosulcate aroid grains can be assumed to be heteropolar. The sulcus is very probably distal rather than proximal, since this is the typical condition for monocots in general (Kuprianova, 1969; Walker



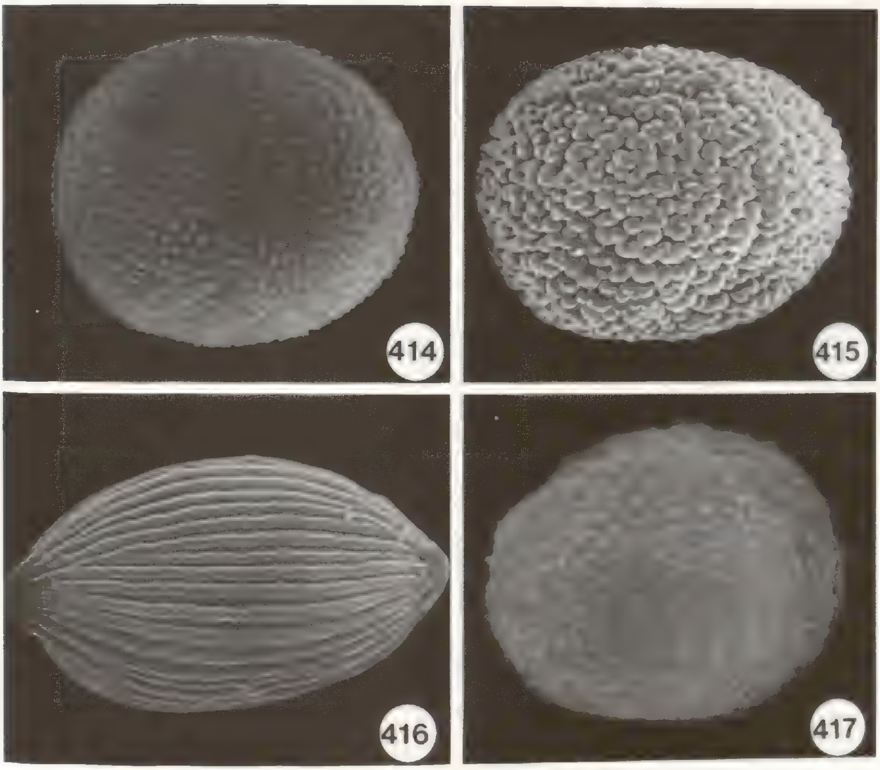
FIGURES 398–403. Monosulcate, subulcerate, and monosulcoidate aroid pollen types (monosulcate except where stated). 398. *Acorus calamus* [Acoraceae] (PS-1); subulcerate. ×3,110. 399. *Gymnostachys anceps* (P-3293). ×2,470. 400. *Pothos scandens* (P-3294). ×4,620. 401. *Orontium aquaticum* (PS-145). ×1,250. 402. *Dracontium asperum* (P-3626). ×2,270. 403. *Stylochaeton natalensis* (P-3717); monosulcoidate. ×1,130.



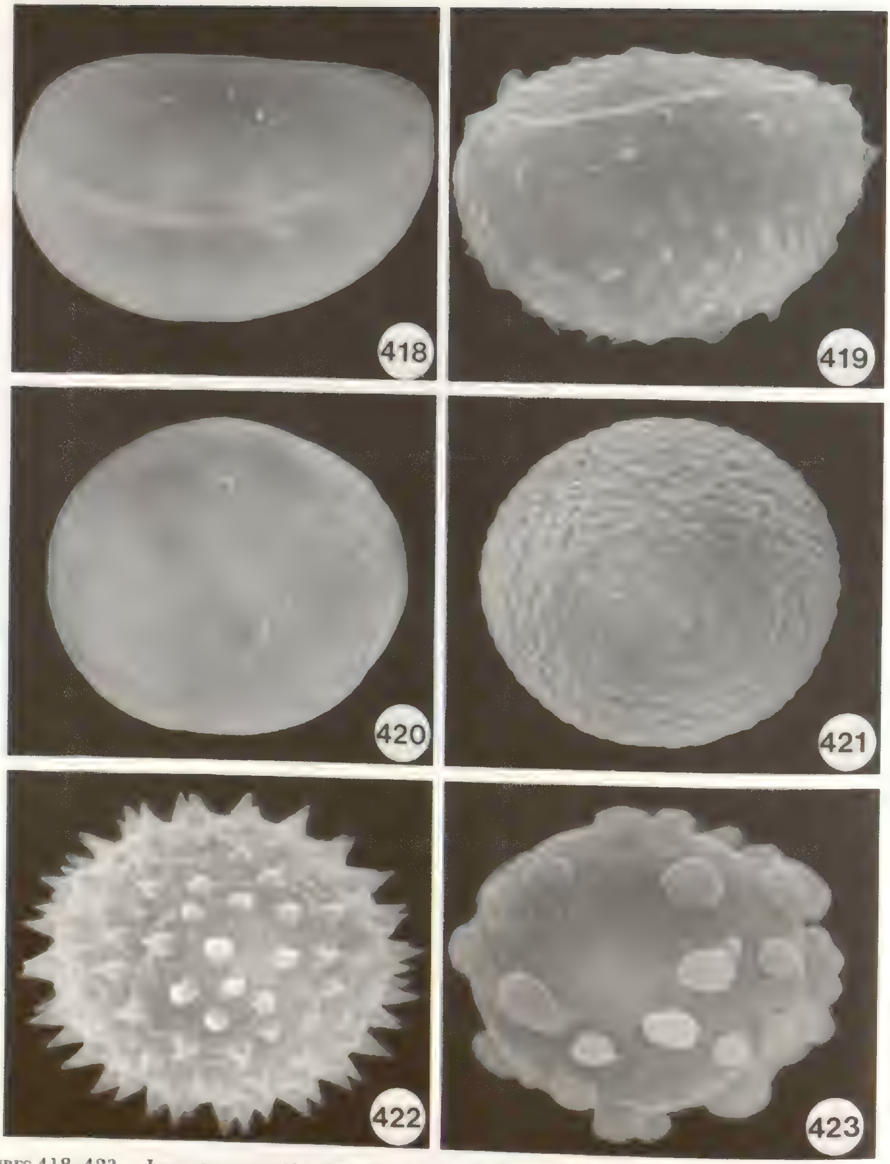
FIGURES 404–409. Extended monosulcate and zonate aroid pollen types (zonate except where stated). 404. *Zamioculcas zamiifolia* (PS-151); extended monosulcate. ×1,000. 405. *Gonatopus angustus* (PS-274). ×940. 406. *Monstera diversifolia* (PS-386). ×1,790. 407. *Stenospermation multiovulatum* (PS-207); zonate with highly reduced nonapertural halves. ×1,190. 408, 409. *Epipremnum pinnatum* (P-3605). Fig. 408, ×2,200. Fig. 409 shows the strongly heteromorphic exine sculpturing on the two nonapertural halves.



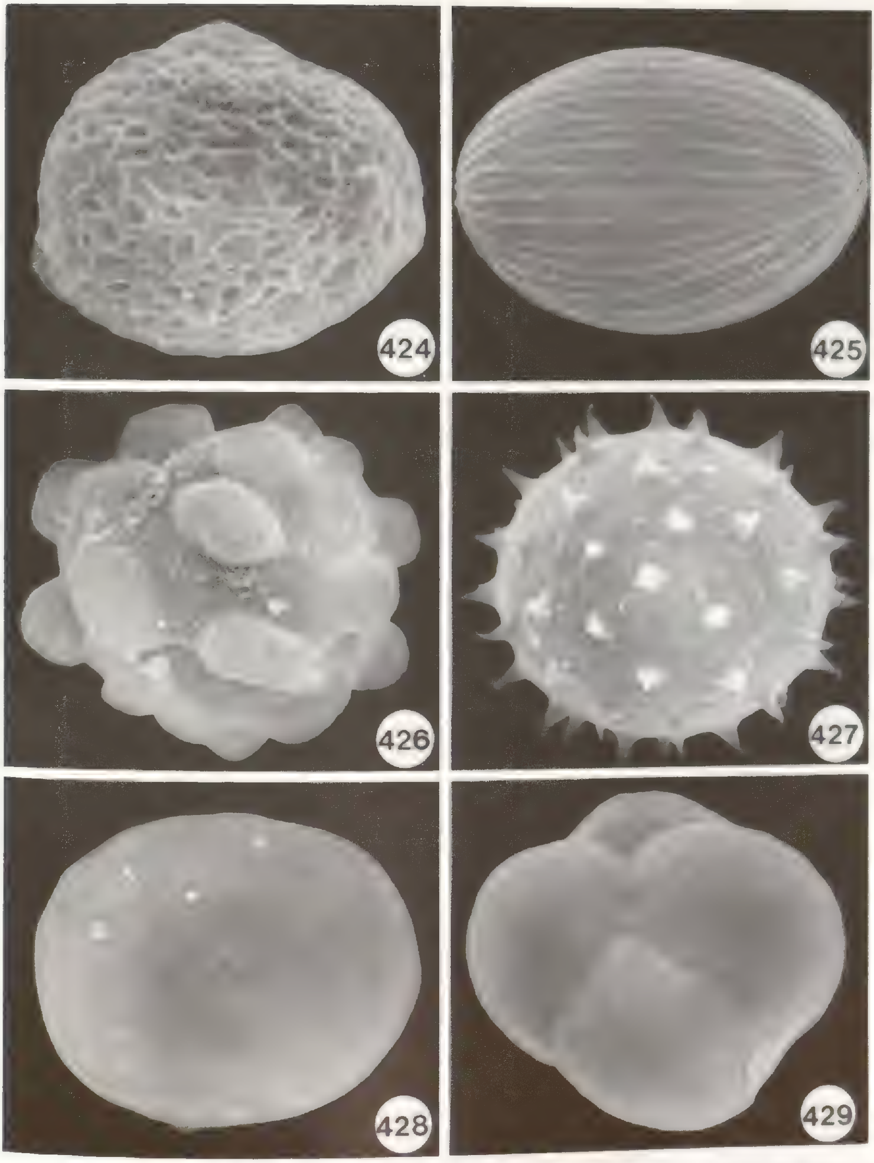
FIGURES 410–413. Diaperturate and forate aroid pollen types (diaperturate except where stated). 410. *Heteropsis integerrima* (PS-192). ×1,330. 411. *Rhaphidophora peeploides* (P-3544). ×2,780. 412. *Calla palustris* (PS-13). ×2,990. 413. *Anthurium pallidiflorum* (PS-156); forate. ×4,220.



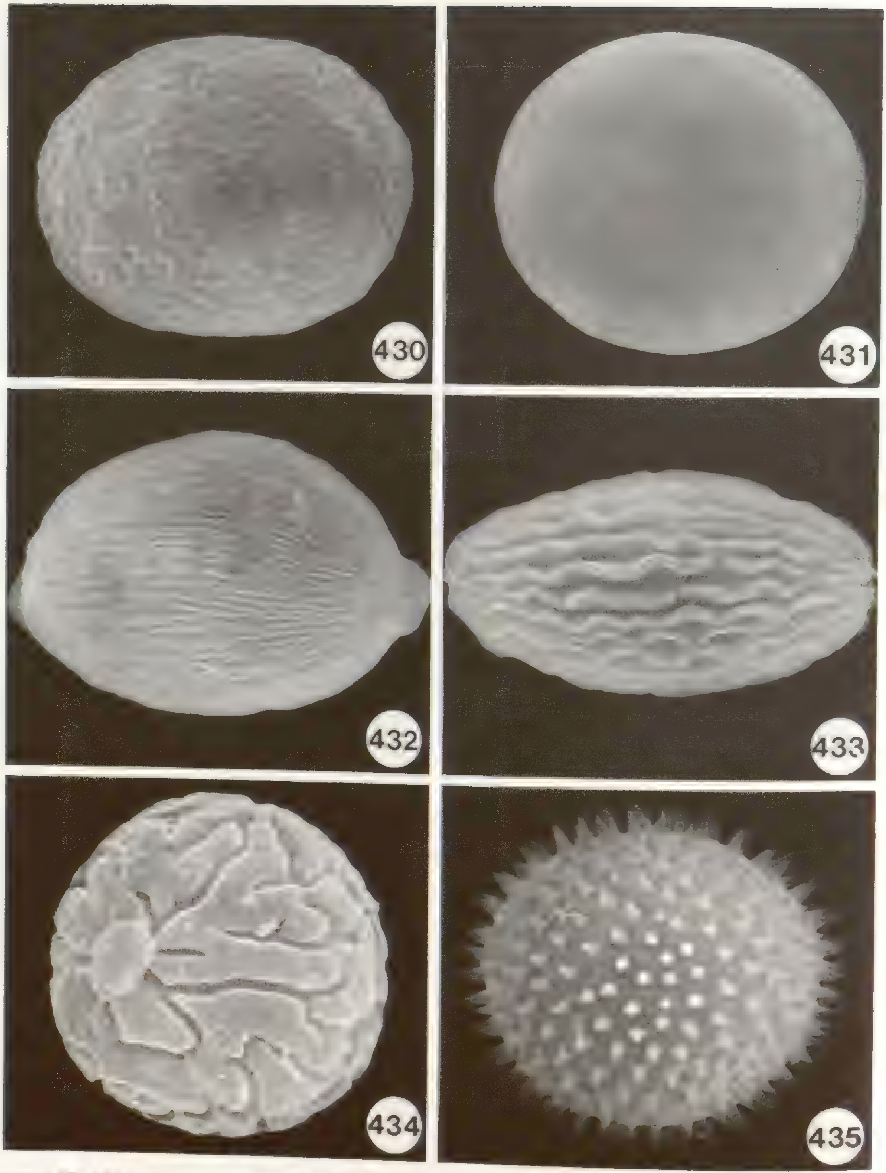
FIGURES 414–417. Inaperturate aroid pollen types: Pothoideae (414, 415) and Monsteroideae (416, 417). 414. *Culcasia longevaginata* (PS-238). ×1,415. 415. *Anadendrum montanum* (PS-176). ×3,695. 416. *Spathiphyllum kalbreyeri* (P-3612). ×2,020. 417. *Stenospermation* sp. indet. (P-3542). ×2,170.



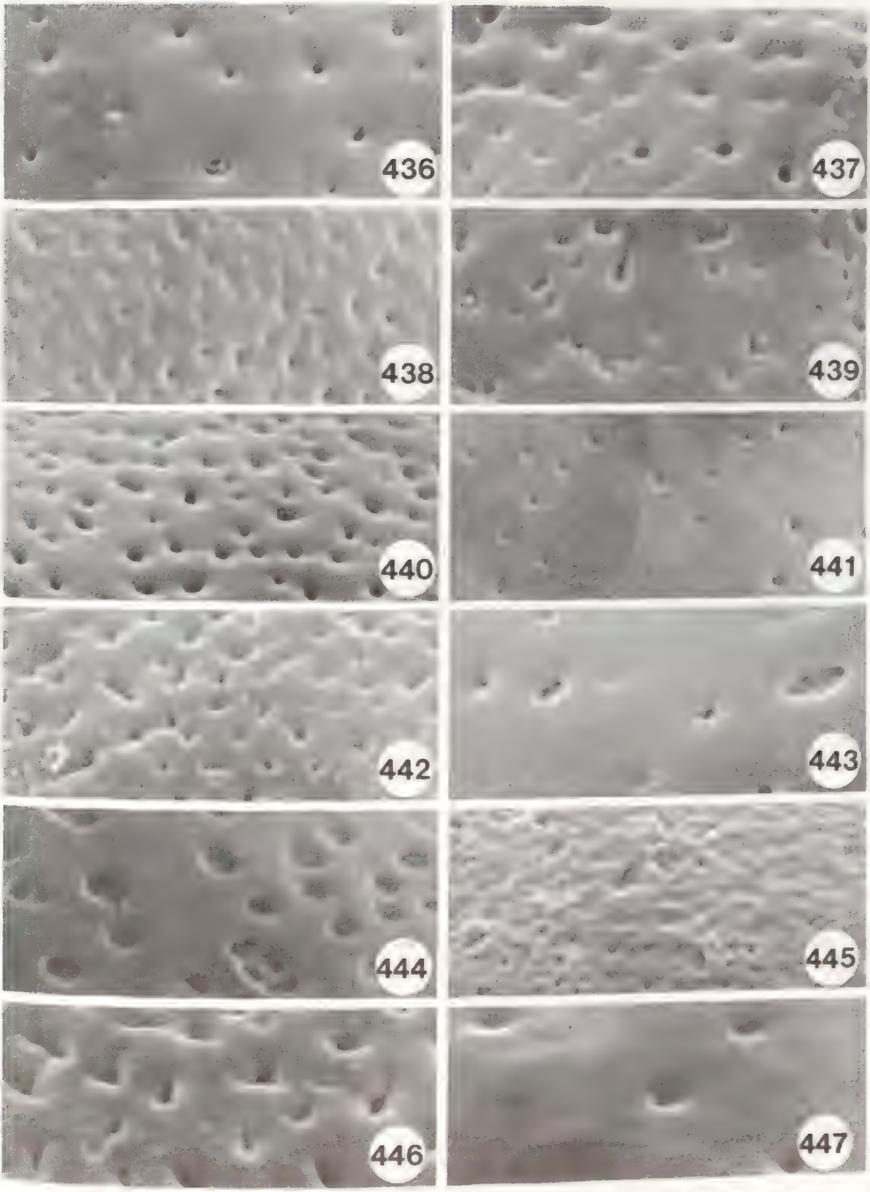
Figures 418–423. Inaperturate aroid pollen types: Philodendroideae. 418. *Asterostigma riedelianum* (PS-438). ×1,910. 419. *Taccarum cardenasianum* (P-3565). ×1,600. 420. *Phymatarum borneense* (PS-140). ×2,980. 421. *Nephthytis afzelii* (PS-240). ×1,190. 422. *Colletogyne perrieri* (PS-135). ×1,680. 423. *Dieffenbachia parlatorei* (P-3686). ×680.



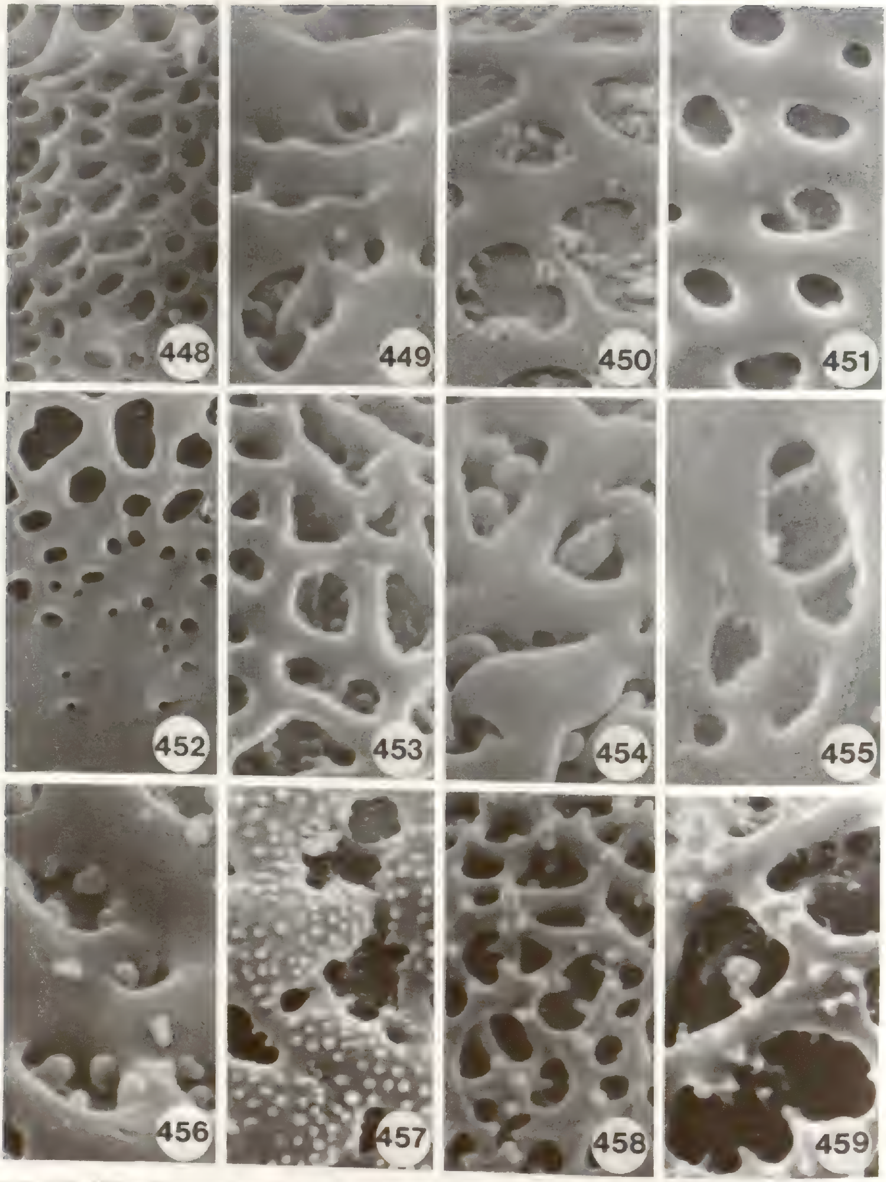
FIGURES 424–429. Inaperturate aroid pollen types: Colocasioideae. 424. *Jasarum steyermarkii* (P-3708). ×1,630. 425. *Steudnera discolor* (PS-199). ×2,980. 426. *Syngonium standleyanum* (PS-366). ×1,370. 427. *Alocasia portei* (PS-373). ×1,420. 428. *Syngonium birdseyanum* (PS-427). ×1,230. 429. *Xanthosoma striatipes* (PS-434); tetrad. ×770.



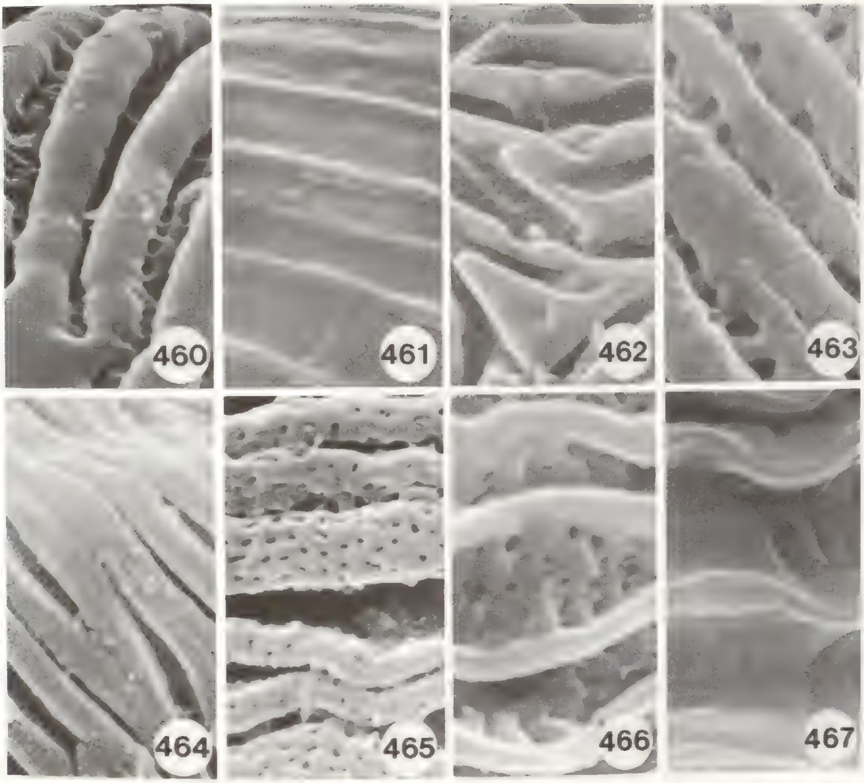
FIGURES 430–435. Inaperturate aroid pollen types: Aroideae. 430. *Stylochaeton zenkeri* (PS-244). ×1,360. 431. *Amorphophallus titanum* (PS-99). ×850. 432. *Pseudodracontium siamense* (PS-413). ×1,335. 433. *Pistia stratiotes* (PS-98). ×2,470. 434. *Amorphophallus konjac* (PS-15). ×1,800. 435. *Typhonium trilobatum* (PS-324). ×2,060.



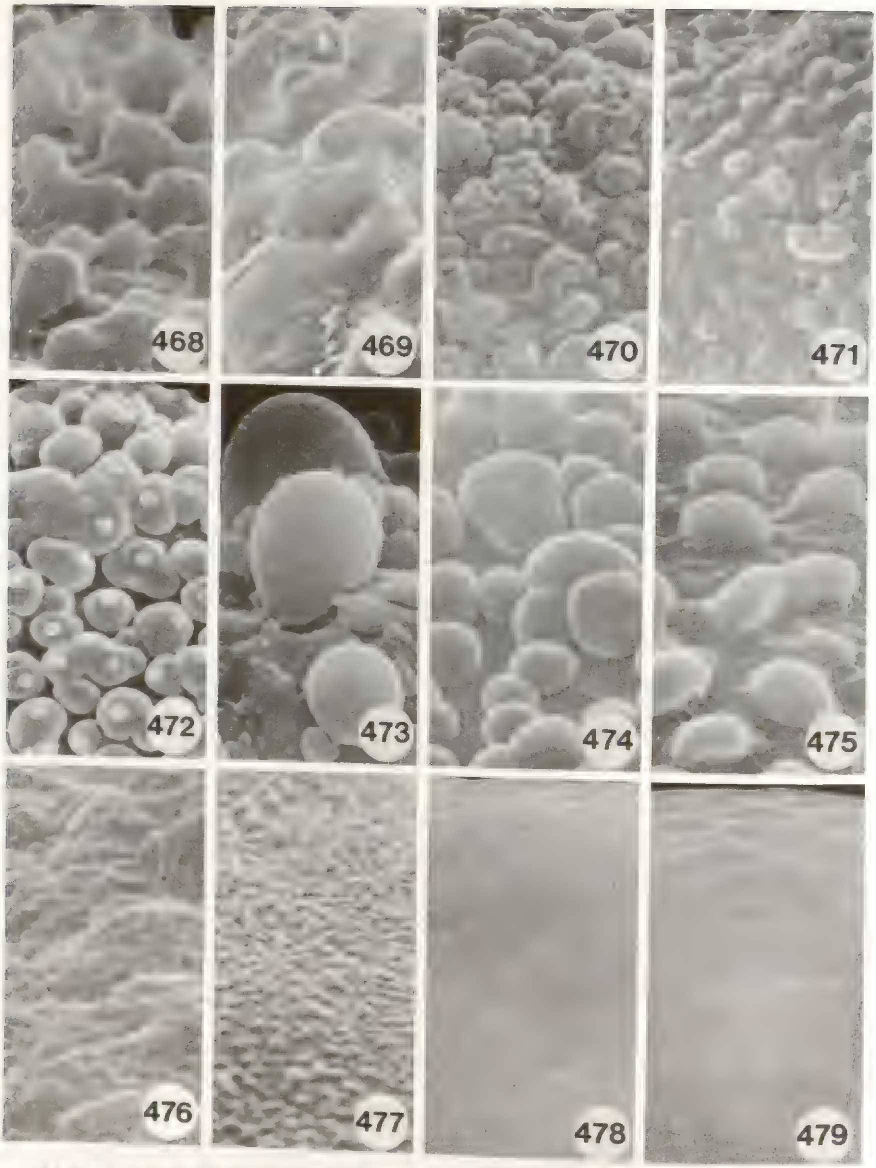
FIGURES 436–447. Microreticulate to foveolate or punctate aroid exine surfaces. 436. *Acorus calamus* [Acoraceae] (PS-1). 437. *Gymnostachys anceps* (P-3293). 438. *Pothos scandens* (P-3294). 439. *Heteropsis oblongifolia* (PS-359). 440. *Monstera skutchii* (P-3601). 441. *Rhodospatha oblongata* (PS-416). 442. *Orontium aquaticum* (PS-145). 443. *Anaphyllopsis americana* (PS-452). 444. *Dieffenbachia pittieri* (P-3683). 445. *Xanthosoma pilosum* (PS-398). 446. *Stylochaeton bogneri* (PS-243). 447. *Amorphophallus titanum* (PS-99).



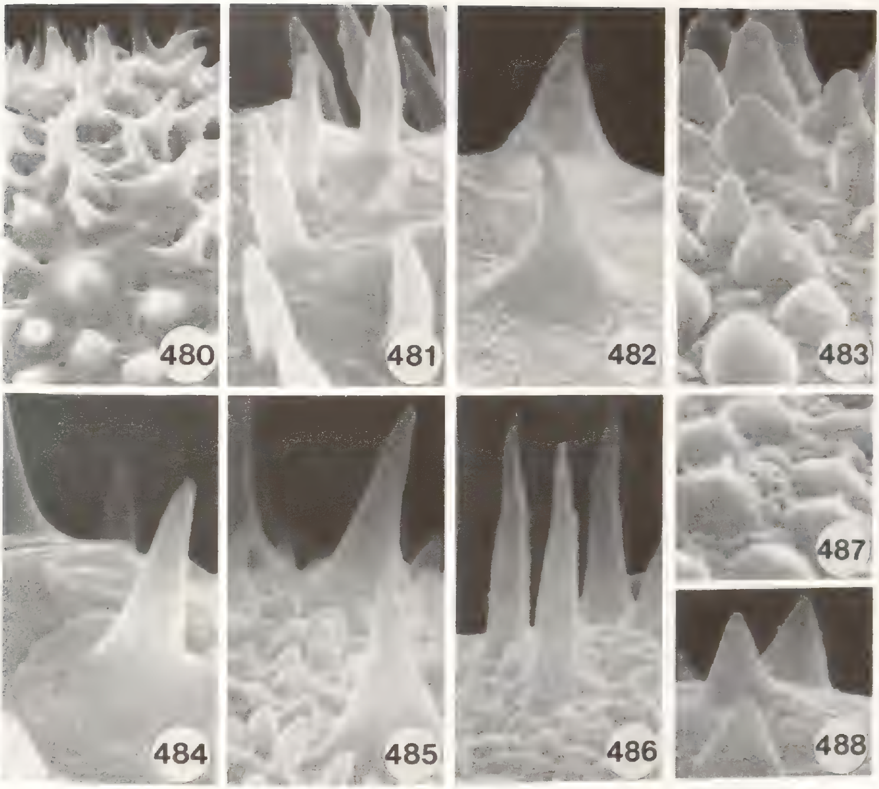
FIGURES 448–459. Reticulate aroid exine surfaces. 448. *Pothoidium lobbianum* (P-3536). 449. *Gonatopus angustus* (PS-274). 450. *Anthurium magnificum* (PS-276). 451. *Monstera adansonii* var. *laniata* (P-3598). 452. *Lysichiton americanus* (PS-16). 453. *Lasia spinosa* (P-3621). 454. *Pycnospatha arietina* (PS-415). 455. *Chlorospatha croatiana* subsp. *croatiana* (PS-249). 456. *Stylochaeton zenkeri* (PS-244). 457. *Anthurium amazonicum* (P-3767). 458. *Anthurium harrisii* (PS-215). 459. *Anthurium redolens* (PS-224).



FIGURES 460–467. Striate aroid exine surfaces. 460. *Spathiphyllum laeve* (PS-114). 461. *Steudnera discolor* (PS-199). 462. *Colocasia indica* (PS-160). 463. *Amorphophallus longituberosus* (P-3635). 464. *Protarum sechellarum* (PS-412). 465. *Arisarum vulgare* (PS-10). 466. *Ambrosina bassii* (PS-118). 467. *Pistia stratiotes* (PS-98).



FIGURES 468–479. Retiverrucate, gemmate, verrucate, scabrate, and psilate aroid exine surfaces. 468. *Culcasia longevaginata* (PS-238). 469. *Gorgonidium vargasii* (PS-459). 470. *Rhaphidophora reineckei* (P-3595). 471. *Podolasia stipitata* (P-3622). 472. *Anadendrum montanum* (PS-176). 473. *Anthurium clidemioides* (PS-109). 474. *Philodendron leal-costae* (PS-410). 475. *Typhonium trilobatum* (PS-324). 476. *Typhonodorum lindleyanum* (PS-507). 477. *Taccarum weddellianum* (PS-143). 478. *Furtadoa sumatrensis* (PS-458). 479. *Chlorospatha corrugata* (PS-134).



FIGURES 480–488. Spinose and spinulose aroid exine surfaces. 480. *Anthurium friedrichsthalii* (P-3755). 481. *Ulearum sagittatum* (P-3711). 482. *Zomicarpa riedeliana* (PS-291). 483. *Callopsis volkensii* (PS-159). 484. *Colocasia esculenta* (PS-14). 485. *Gonatanthus sarmentosus* (P-3696). 486. *Theriophonum infaustum* (PS-417). 487. *Pinellia cordata* (PS-97). 488. *Arisaema lichiangense* (P-3792).

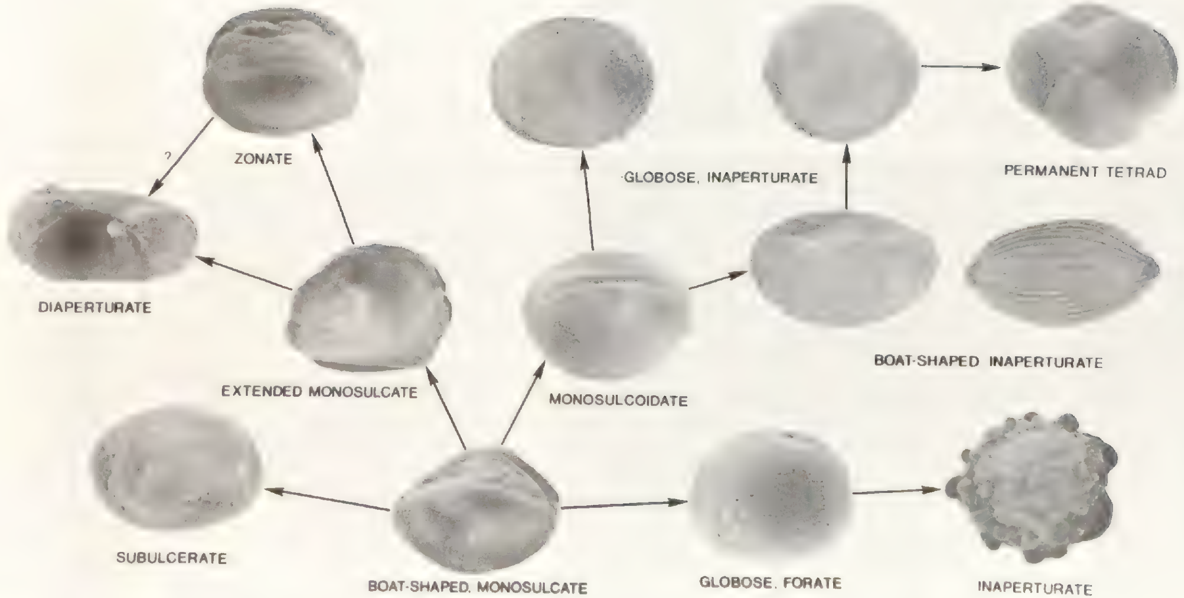


FIGURE 489. Scheme for the evolution of aperture types, pollen shape, and pollen unit in the Araceae. Examples are as follows: boat-shaped, monosulcate = *Gymnostachys anceps*; subulcerate = *Acorus calamus* [Acoraceae]; extended monosulcate = *Zamioculcas zamiifolia*; diaperturate = *Heteropsis integerrima*; zonate = *Epipremnum pinnatum*; globose, forate = *Anthurium pallidiflorum*; inaperturate (forate-derived) = *Anthurium clidemioides*; monosulcoidate = *Stylochaeton natalensis*; globose, inaperturate = *Stylochaeton zenkeri* (left) and *Dieffenbachia pittieri* (right); boat-shaped, inaperturate = *Philodendron leal-costae* (left) and *Spathiphyllum kalbreyeri* (right); permanent tetrad = *Xanthosoma striatipes*. Pollen of the examples chosen is thought to have evolved in the manner depicted, but not from the other extant taxa in the diagram.

& Doyle, 1975). Thus, monosulcate grains of Araceae may confidently be specified as anasulcate and very likely would appear in the tetrad stage much like the pollen of *Philydrella* (Fig. 554) of the Philydraceae.

Monosulcate pollen may be described as boat-shaped and bilaterally symmetrical. Inasmuch as monosulcate pollen has already been shown to embody the primitive aperture type in Araceae, it may be assumed that the heteropolar, boat-shaped, and bilaterally symmetric conditions—all intimately correlated with the monosulcate aperture type (Walker & Doyle, 1975)—represent the most primitive stages of polarity, pollen shape, and pollen grain symmetry, respectively, in Araceae. Boat-shaped/elliptic grains are the commonest of the various subtypes in monosulcate Araceae, and this probably represents the most primitive subtype. The other extreme, boat-shaped/elongate (Fig. 256), is unusual and must be considered derived.

An analysis of the situation in zonate and diaperturate aroid pollen must depend on the scheme for the evolution of these aperture types discussed previously. Assuming that extended monosulcate apertures have evolved via the elongation of a distal sulcus, it is logical to suppose that the "hinge" of extra-apertural exine on such a grain overlies the position of the proximal pole. Thus, referring to Figure 404, the polar axis must pass through this hinge at an angle more or less perpendicular to the plane of the figure. In a fully zonate grain, the polar axis would be indistinguishable beyond the tetrad stage, one of the infinite number of axes lying in the plane of the aperture. The axis connecting the centers of the two extra-apertural exine halves must thus be regarded as one of the equatorial axes. Since the aperture in zonate aroid pollen is thus most probably meridional, it may be more precisely described as zonasulcate (equivalent to the "meridionosulcate" of earlier authors). This was Thanikaimoni's (1969) conclusion for zonate aroid pollen, but it is unclear if this was based on conjecture or on examination of tetrads.

One implication of these considerations is that, although extended monosulcate pollen must still be described as heteropolar, this is not true of fully zonate pollen. Zonate grains must rather be designated as isopolar or subisopolar, the latter term being generally employed here since in most grains the meridional circumference does not appear to form a perfect circle. Shape and symmetry in zonate grains can be difficult to resolve. The length of the polar axis relative to the equatorial axes is generally impossible to determine in single grains inasmuch as the polar axis cannot be identified. By analogy with typical monosulcate grains, one might suppose that the polar axis would usually represent the shortest axis in the apertural plane; however, in the extended monosulcate grain of *Rhaphidophora reineckei* illustrated in Figure 80, the putative polar axis is the longest axis in the plane. Thus, going strictly by definition, pollen of this particular species would fall into the globose, prolate shape category (cf. Walker & Doyle, 1975). This is not always the case, however; zonate pollen of other species might even have to be described as boat-shaped if the polar axis can be demonstrated to be relatively short. Since the situation in all species is entirely ambiguous, I have resorted to the graphic and noncommittal term "hamburger-shaped" for describing the shape of zonate aroid pollen grains.

One might expect that typical bilateral symmetry, as seen in monosulcate pollen, would also prevail in extended monosulcate and zonate aroid pollen. This is seldom the case, but see pollen of *Stenospermation multiovulatum* (Fig. 111) and *Scindapsus splendidus* (Fig. 105), which is essentially isobisymmetric. There is a strong tendency toward heteromorphy, such that one of the two original vertical planes of symmetry is lost, in the two extra-apertural exine halves of zonate grains. Pollen grain symmetry in species with zonate pollen might be described simply as "bilateral," since it is in most cases truly bilateral (i.e., with but a single vertical plane of symmetry); unfortunately, however, that term has traditionally been reserved for the type of symmetry exhibited by monosulcate grains, which ought to be termed "anisobisymmetric" (Walker & Doyle, 1975). Rather than attempting to buck tradition, it has been decided to employ the designation "monosymmetric" (Walker & Doyle, 1975) for truly bilaterally symmetric zonate grains in Araceae and to conserve "bilateral" for typical monosulcate grains.

The most plausible scenario for the evolution of diaperturate grains—i.e., directly from extended monosulcate grains—entails a distal closure of the sulcus, at a point more or less opposite the proximal "hinge." Thus the two apertures are envisioned as being equatorial rather than polar. Since the apertures must also be meridional, diaperturate aroid pollen might be described more precisely as dicolpate, or perhaps as diporate in the case of *Rhaphidophora peeploides* (Fig. 411). This notion receives some support from Thanikaimoni (1970), who apparently studied polarity at the tetrad stage in palms and claimed never to have observed diaperturate pollen with one distal and one proximal furrow.

The polar axis in diaperturate aroid pollen does not pass through the apertures, according to the above scenario; the line connecting the apertures must rather represent an equatorial axis. In either case, all diaperturate grains must be described as isopolar or subisopolar rather than heteropolar. The grains of *Heteropsis integerrima* (Fig. 410) and *Rhaphidophora peeploides* (Fig. 411), which have an elongate equatorial axis and a short and indistinguishable polar axis, must be classed as boat-shaped. Pollen of *Calla palustris* (Figs. 133, 134), on the other hand, is essentially globose. Judging from the orientation of the individual apertures, the polar axis is thought to traverse the grain horizontally in Figure 133, and perpendicular to the plane of Figure 134.

Diaperturate pollen in Araceae is to be regarded as bilaterally symmetrical, or in *Calla* essentially isobisymmetric.

The forate aperture type, as seen in *Anthurium*, exemplifies the phenomenon of peripory, defined as a tendency toward a more or less regular arrangement of apertures. This tendency is closely associated with the transition to globose or spherical grains (Van Campo, 1976). The term "forate" has been used in *Anthurium* since the pores are seldom observed to be in a single plane. Polarity in *Anthurium* is generally apolar, the pollen shape is spherical or subspheroidal, and symmetry is most conveniently designated as radiosymmetric, although in many cases pollen of *Anthurium* may be technically asymmetrical due to the irregular distribution of pores.

Spherical or subspheroidal inaperturate pollen in Araceae presents no problems with regard to polarity, shape, and symmetry. It may simply be described as apolar, spherical, and radiosymmetric. Pollen of this type is most common in Colocasioideae and Aroideae and is especially typical of grains with spinose exine sculpturing. It is also to be seen, however, in Pothoideae (*Culcasia*, *Anadendrum*), Lasioideae (numerous species of *Amorphophallus*, *Nephthytis*), and Philodendroideae (*Dieffenbachia*, *Peltandra*, and other genera). Occasionally, inaperturate, subspheroidal grains may bear exinous protuberances of such magnitude (see Figs. 423, 426) that the grains might be considered asymmetric.

A greater problem is represented by elongate, inaperturate grains. These occur, for example, in *Spathiphyllum* (Fig. 416), the Thomsonieae (Fig. 432), *Anchomanes* (Fig. 266), *Pseudohydrosme* (Fig. 268), most of the Philodendroideae (e.g., Fig. 172), *Steudnera* (Fig. 425), *Colocasia* (Fig. 308), the Spathicarpeae (e.g., Fig. 418), *Arisarum* (Fig. 392), *Ambrosina* (Fig. 394), the Cryptocoryninae (Fig. 222), and *Pistia* (Fig. 433). Ordinarily one might consign such pollen to the globose, prolate category without further ado. Prolate pollen has a prominent polar axis that is longer than the subequal equatorial axes (Walker & Doyle, 1975). In *Spathiphyllum*, however, Huynh (1975) has demonstrated from studies on pollen tetrads in *S. wallisii* that the longest axis is actually an equatorial axis; the polar axis is not distinguishable, being one of the infinite subequal shorter axes. Thus the pollen of *Spathiphyllum* conforms perfectly to the definition for "boat-shaped" (Walker & Doyle, 1975).

Although the terms "boat-shaped" and "monosulcate" have come to be inseparably associated with one another, probably because of the strong negative correlation between the "globose" and "monosulcate" conditions, there is no reason why boat-shaped, inaperturate pollen should not exist. Indeed, in an evolutionary scenario such as that being proposed for Araceae—i.e., in which a pervasive trend from boat-shaped, monosulcate to globose, inaperturate pollen is conceived—boat-shaped, inaperturate pollen is a logical intermediate stage. In most other families, however, globose, aperturate pollen appears to represent the intermediate stage in this same transformational sequence (J. Walker, pers. comm.).

Although the only direct evidence for boat-shaped, inaperturate pollen in Araceae comes from Huynh's work on *Spathiphyllum*, other indications hint that this condition may be more widespread. On pollen of many Araceae with elongate, inaperturate grains, a longitudinal raphe or keel can be seen on one face. This is most strikingly developed in *Philodendron callosum* (Figs. 198, 199); however, it may be seen in most species of *Philodendron* and in other genera of the subfamily Philodendroideae (Figs. 167, 178, 196, 206, 208) as well as in *Amorphophallus bulbifer* (Fig. 384), *Cercestis*, many Spathicarpeae (Figs. 239, 248, 250, 254, 256), and Cryptocoryninae (Figs. 222, 223, 225). Occasionally such a keel is even evident on globose grains, as in *Dracunculus vulgaris* (Fig. 336).

It is suggested here that the keeled or faceted nature of the aforementioned grains is a direct result of their orientation within the tetrad; that the keeled face represents the proximal face; that the longest axis is therefore an equatorial axis; and thus that grains of this type are truly boat-shaped. That the shape of pollen grains is determined in part by the manner of pollen mother-cell cytokinesis and the orientation of grains in the tetrad has been appreciated since the time of Fischer (1890).

Successive pollen mother-cell cytokinesis, which is apparently general in Araceae, typically yields pollen grains with a "primary form" that is remarkably similar to that of mature pollen of *Philodendron callosum* (Fig. 199). Tammes (1930) illustrated this "primary form" (see his fig. 2), terming it a "spherical-wedge"; he noted that "as a rule the primary form of the pollen is not preserved long," as the cells tend to "grow rounded." It is conceivable that the retention of this "primary form" in some Araceae, the concomitant failure of the aperture to develop, and perhaps even the tendency for pollen of these species to have a psilate exine may all be explainable on the basis of neoteny.

That the keeled rather than the convex face of the "primary form" represents the proximal face of the grain is evident from geometrical considerations alone. A further supporting example is the occasional occurrence of a longitudinal keel on what is clearly the proximal face of aperturate grains, as in the monosulcate pollen of *Dracontium polyphyllum* (Fig. 158) or the monosulcoidate pollen of *Stylochaeton natalensis* (Fig. 327). Outside the Araceae, such a keel can be seen on pollen of species in Pandanaceae; in *Freycinetia excelsa* (Fig. 529) the presumably distal aperture can be seen on the convex face of the grain, i.e., opposite the keeled face.

Thus it is highly probable that most elongate, inaperturate pollen in Araceae is boat-shaped rather than prolate, and this assumption has been made consistently in the generic pollen descriptions with the realization that some prolate pollen may be incorrectly described. It is clear that much more work is needed on the tetrad stage to establish absolute polarity of the various araceous pollen types.

Boat-shaped, inaperturate aroid pollen must be considered isopolar, or subisopolar in cases where the equatorial plane is somewhat curved, i.e., where one polar face is more convex than the other. This is frequently the case (see Figs. 197, 256 for extreme examples), which is not surprising since most monosulcate grains would probably have to be considered subisopolar if the aperture were ignored. All boat-shaped, inaperturate grains are bilaterally symmetrical (i.e., anisobisymmetric) or essentially so.

To summarize the foregoing conclusions regarding the evolution of polarity, pollen shape, and pollen grain symmetry in Araceae (see also Fig. 489): the most primitive aroid pollen is heteropolar, boat-shaped-elliptic, and bilaterally symmetrical; apolar pollen was derived from heteropolar pollen via subisopolar and isopolar intermediate stages (or in *Anthurium* perhaps directly). Boat-shaped grains have given way through gradual equalization of the axes to subspheroidal and spherical grains. Concomitant with this has been a gradual transition from bilateral to radial symmetry. Those few pollen types having isobisymmetric (*Calla*, Fig. 134; *Scindapsus*, Fig. 105; *Stenospermation multiovulatum*, Fig. 111) or monosymmetric pollen (e.g., some *Heteropsis* species and most Monstereae) represent an evolutionary side branch derived from the bilateral type. There is no evidence that any of the above trends is reversible.

Boat-shaped, inaperturate pollen is believed to be widespread in Araceae, and represents an evolutionary stage intermediate between the boat-shaped, monosulcate and globose, inaperturate stages. Neoteny may have played a role in the evolution of boat-shaped, inaperturate pollen from monosulcate ancestors, at least in some cases.

POLLEN UNIT

Pollen of all aroid genera is shed in monads, except for *Xanthosoma* and *Chlorospatha* (Figs. 282–289), in which pollen is shed in permanent tetrads. This is one case where ontogeny surely does not recapitulate phylogeny. Even though all pollen grains originate in tetrads as a result of meiosis, most often they are released singly from the anther locules. Monads are considered basic for angiosperms as a whole. Although tetrads or polyads are basic and perhaps primitive in some families, and may even give rise to monads secondarily (Walker & Doyle, 1975), there is no basis for proposing any such scenario in Araceae. While there is a general correlation between the shedding of pollen in tetrads and the production of a large number of ovules (Walker, 1971), which holds up fairly well for *Xanthosoma* and *Chlorospatha*, and it is also true that high ovule number is generally considered to be a primitive character, many other aroids have high ovule numbers yet shed pollen in monads. Were permanent tetrads primitive for Araceae as a whole, the latter fact would be difficult to explain.

The tetrads in *Xanthosoma* and *Chlorospatha* are tetragonal or obscurely decussate, which is typical of monocots as a whole (Maheshwari, 1949; Walker & Doyle, 1975). They are unusual, however, in that they have almost reached the point of becoming "cryptotetrads," i.e., the limits of the individual grains are scarcely discernible externally. Outside of these genera, a chance tetrad was observed only once (in *Colocasia esculenta*, of the same subfamily: it was decussate). In other mono-

TABLE 2. Comparison of pollen measurements from light slides and SEM micrographs.

		Mean diameter (μm)		
Sample number	Species	From light slide	From SEM micrograph	% Shrinkage
P-3576	*Pothos remotiflorus*	16	12	25.0%
PS-238	*Culcasia longevaginata*	40	36	10.0%
PS-424	*Aglaonema simplex*	37	32	13.5%
PS-150	*Aridarum nicolsonii*	21	14	33.3%
P-3711	*Ulearum sagittatum*	26	26	0.0%
P-3534	*Gorgonidium mirabile*	41	35	14.6%
PS-494	*Anchomanes nigritianus*	94	58	38.3%
P-3639	*Anchomanes* sp. indet.	61	50	18.0%
P-3553	*Montrichardia arborescens*	92	56	39.1%
PS-159	*Callopsis volkensii*	37	24	35.1%
PS-199	*Steudnera discolor*	22	20	9.1%
PS-380	*Typhonium blumei*	28	20	28.6%
PS-326	*Biarum tenuifolium*	30	22	26.7%
PS-275	*Pinellia tripartita*	29	23	20.7%
PS-232	*Amorphophallus lambii*	60	45	25.0%
P-3641	*Amorphophallus variabilis*	43	40	7.0%
		Average shrinkage:		21.5%

cot families, tetrads occur most notably in Velloziaceae, Juncaceae, Cyperaceae, Typhaceae, Philydraceae (Fig. 554), and Orchidaceae; dyads are found in Scheuchzeriaceae (Fig. 571) (Fischer, 1890; Erdtman, 1945; Walker & Doyle, 1975).

POLLEN SIZE

Size of pollen is a notoriously unreliable taxonomic character. Pollen grains are well known for their ability to expand and contract under different environmental or laboratory conditions (Wodehouse, 1935). Measurements of pollen from the same aroid species provided by different literature sources often vary widely. Since no description of the treatment to which such pollen has been exposed is generally given, no attempt has been made in this report to incorporate size data from the literature.

During the present investigations, pollen size was measured from light slides prepared under uniform conditions. In a few cases size had to be calculated directly from SEM micrographs, which yield consistently smaller measurements. The extent of SEM shrinkage is unpredictable and may vary from 0 to 40%, depending on the characteristics of the pollen. Table 2 provides measurements made under SEM and light microscope conditions for a range of species selected for comparison with taxa for which pollen size had to be calculated from SEM micrographs.

Pollen size also varies according to chromosome number, or, more probably, chromatin content. This is true both interspecifically (Löve & Löve, 1975; Taylor & Levin, 1975; Muller, 1979) and intraspecifically. Different chromosomal races within a species would be expected to have different sizes of pollen, and Henny (1979) has reported a very small percentage of outsized pollen grains that he attributed to nondisjunction in each of several *Dieffenbachia* species. Muller (1979) reported that pollen size may also vary according to the quality of mineral nutrition, local climate, and other environmental factors. Such factors may have occasionally complicated attempts to obtain standardized pollen measurements.

Pollen size data for genera of Araceae are presented hierarchically in Table 3, after the manner of Walker (1971) (see also Table 1, which summarizes pollen data, including size, in a taxonomic format).

The overall mean size for araceous pollen is about 37 μm. The majority of generic means (68%) fall into the "medium-sized" category; 19% are considered "small," and 12% "large." Only *Pseudohydrosme* has pollen classified as "very large." No Araceae are yet known with pollen in either the "minute" (less than 10 μm) or "gigantic" (200 μm or greater) size classes of Walker & Doyle (1975).

Four peaks appear in the distribution of generic size means for araceous pollen: 22–26 μm; 32–33 μm; about 40 μm; and 45–48 μm. The significance of these peaks is unknown.

The smallest aroid pollen yet known, as measured from light slides, is 12 μm, from *Homalomena*

TABLE 3. Aroid genera arranged in ascending order of pollen size.

	Small grains (10–24 µm)
*14	*Hottarum*
17	*Furtadoa*
*18	*Pedicellarum*
18	*Podolasia*
*19	*Phymatarum*
*(19)	*Zomicarpella*
20	*Schismatoglottis*
20	*Ariopsis*
21	*Pothos*
*21	*Filarum*
*21	*Protarum*
22	*Anadendrum*
22	*Anthurium*
22	*Lasimorpha*
22	*Homalomena*
22	*Steudnera*
22	*Arisaema*
23	*Calla*
23	*Dracontioides*
23	*Aridarum*
24	*Anubias*
	Medium-sized grains (25–49 µm)
25	*Piptospatha*
25	*Colocasia*
25	*Pinellia*
*25	*Theriophonum*
26	*Pothoidium*
26	*Urospatha*
26	*Ulearum*
26	*Chlorospatha*[1]
27	*Lasia*
27	*Pistia*
29	*Cyrtosperma*
29	*Anaphyllum*
*(29)	*Bucephalandra*
30	*Biarum*
31	*Gymnostachys*
31	*Anaphyllopsis*
32	*Culcasia*
32	*Spathiphyllum*
32	*Zomicarpa*
32	*Arophyton*
32	*Gonatanthus*
32	*Arum*
32	*Typhonium*
33	*Holochlamys*
33	*Rhaphidophora*
33	*Symplocarpus*
33	*Peltandra*
33	*Remusatia*
33	*Sauromatum*
34	*Pycnospatha*
34	*Cryptocoryne*
34	*Carlephyton*
34	*Gorgonidium*
35	*Alocasia*
36	*Dracontium*
36	*Lagenandra*
36	*Asterostigma*
37	*Callopsis*
*(37)	*Lazarum*
38	*Scindapsus*
39	*Amydrium*
39	*Colletogyne*
40	*Heteropsis*
40	*Epipremnum*
40	*Lysichiton*
40	*Zantedeschia*
40	*Philodendron*
(40)	*Mangonia*
40	*Hapaline*
42	*Stenospermation*
42	*Xanthosoma*[1]
*43	*Cercestis*
43	*Caladium*
44	*Jasarum*
44	*Eminium*
44	*Ambrosina*
45	*Typhonodorum*
45	*Scaphispatha*
45	*Dracunculus*
45	*Arisarum*
46	*Alloschemone*
*46	*Nephthytis*
47	*Rhodospatha*
48	*Monstera*
48	*Spathicarpa*
48	*Syngonium*
48	*Pseudodracontium*
49	*Synandrospadix*
	Large grains (50–99 µm)
*52	*Aglaonema*
53	*Stylochaeton*
53	*Amorphophallus*
54	*Spathantheum*
*(56)	*Gearum*
59	*Aglaodorum*
59	*Bognera*
60	*Zamioculcas*
63	*Taccarum*
64	*Orontium*
64	*Anchomanes*
76	*Gonatopus*
79	*Dieffenbachia*
94	*Montrichardia*
	Very large grains (100–199 µm)
*106	*Pseudohydrosme*

Sizes represent mean diameters of all species available.
* = diameters calculated directly from SEM micrographs.
( ) = data from literature or correspondence (see text).
[1] = diameters measured of individual grains, not tetrads.

cf. *versteegii*. Small pollen is especially characteristic of the tribe Potheae, the subtribes Homalomeninae and Schismatoglottidinae, and the large genera *Anthurium* and *Arisaema*, but it occurs in genera of every subfamily except Monsteroideae and Pistioideae. Small pollen may be monosulcate, diaperturate (*Calla*), forate (*Anthurium*), or inaperturate, as well as boat-shaped to spherical. Zonate pollen is never small. All types of exine sculpturing from reticulate to striate (*Steudnera*), spinose, and psilate occur on small pollen.

Large pollen likewise exhibits a range of aperture, shape, and exine sculpturing types. Monosulcate (*Orontium*), zonate (Zamioculcadeae), and inaperturate grains of all shapes and exine types attain large sizes. Although the distribution curve for aroid pollen size drops off precipitously beyond 49 µm, the relatively few genera with large mean pollen size occur in all subfamilies except Monsteroideae, Colocasioideae, and Pistioideae; even within the former two subfamilies certain species are characterized by large pollen. *Pseudohydrosme gabunensis* (Fig. 268) possesses the largest pollen yet discovered in Araceae. This was calculated at 106 µm from SEM micrographs, which would yield a deflated figure relative to most of the other measurements given in Table 3. Indeed, large psilate pollen with similar characteristics in the putatively related *Anchomanes nigritianus* and *Montrichardia arborescens* showed the most shrinkage as a result of processing for SEM of any Araceae for which such information is available. Taking this factor into account, *Pseudohydrosme* pollen measured from light slides might be as large as 180 μm. Bogner (1981a) measured pollen of this species at 100–120 μm; the manner of treatment was not indicated.

The most primitive pollen size range for Araceae ought to be estimable by figuring the mean size of the most primitive pollen type, i.e., boat-shaped, monosulcate pollen. Pollen of this type ranges from about 17 μm (*Pedicellarum*) to 64 μm (*Orontium*); however, there is a rapid attenuation beyond 37 μm, and the mean size of 30 μm is considerably less than the overall mean for aroid pollen. Ignoring *Orontium*, the mean size of monosulcate aroid pollen drops to but 28 μm. This figure compares favorably with the data for most monosulcate pollen of other monocot families gathered during the present study: Arecaceae, 28 μm; Cyclanthaceae, 26 μm; Cyanastraceae, 32 μm; Philydraceae, 33 μm; Triuridaceae, 22 μm; Aponogetonaceae, 23 μm; and Butomaceae, 29 μm. Only Taccaceae, with monosulcate pollen averaging 52 μm, diverge significantly from the norm.

I suggest, therefore, that the primitive pollen size of Araceae lies somewhere in the range of 22–34 μm. Given that there has obviously been a pervasive trend in the direction of larger pollen, undoubtedly involving monosulcate types, the actual figure may well lie toward the lower end of this range. Grains larger than this, certainly 40 μm or above, are viewed as being derived in this regard, as are extremely small grains. Only six aroid genera have mean pollen sizes below 20 μm, and half of these values were calculated from SEM micrographs. Furthermore, very small-grained species in Homalomeninae and Schismatoglottidinae, on one hand, and *Anthurium*, on the other, have obvious specializations in being inaperturate and psilate, or forate, respectively. Pollen size is not independent of shape, since the longest axis is measured, so that the evolutionary transition from boat-shaped to globose pollen, as has presumably happened in *Anthurium*, for example, might result in an apparent decrease in pollen size without change in volume.

Walker & Doyle (1975) suggested that the primitive pollen size for angiosperms lies in the 50–99 μm range, this based on the observation of pollen sizes in the most primitive Magnoliidae. If true, this would imply that the much smaller size of primitive aroid pollen is a derived feature within the Angiospermae.

EXINE SCULPTURING

Nonapertural exine. "The different members of the Arum family furnish beautiful and most peculiar pollen grains, of many diverse characters" (Smith, 1876: 517). The Araceae do indeed constitute an unusually eurypalynous family in all respects, and the resolution of the myriad minute variations in exine sculpturing patterns into a plausible evolutionary framework has represented one of the major challenges of this investigation. But if the family is to be regarded as monophyletic, all of these manifestations must be traceable back to a single primitive type. The conclusions arrived at during the course of these studies are represented diagrammatically in Figure 490, and are discussed in detail below.

The candidates for the most primitive type of exine sculpturing in Araceae were narrowed down using the same reasoning employed to determine the primitive aperture type, that is, in-group analysis and out-group analysis, with reference to the fossil record. The earliest known fossil pollen type recognizable as being monocotyledonous, *Liliacidites*, has reticulate exine sculpturing (Doyle, 1973; Wolfe et al., 1975). Reticulate to foveolate exine is widespread in and probably basic to other monocots having monosulcate pollen, e.g., *Butomus* (Figs. 579, 580), *Aponogeton* (Figs. 563–566), palms (Figs. 503–519), Cyclanthaceae (Figs. 520–521), Bromeliaceae (Ehler & Schill, 1973), Amaryllidaceae (Erdtman, 1952), the lilialean complex (Roth et al., 1987), and Commelinaceae (Poole & Hunt, 1980). Most contemporary authors (e.g., Walker & Doyle, 1975) regard reticulate exine as primitive for monocots. Thanikaimoni (1970), however, believed psilate exine to be the primitive condition in palms (but see also Harley, 1990), and this is supposedly also true for magnoliid dicots (Walker, 1976).

In Araceae, foveolate to reticulate exine sculpturing prevails almost exclusively in genera with monosulcate, and monosulcoidate pollen types, the only exception being the verruculate pollen of *Podolasia* (Fig. 471). Moreover, these exine types are the rule in the remaining aperturate genera—those with forate, zonate, and diaperturate pollen. Reticulate and foveolate exines are unusual, however, in inaperturate aroid pollen; only in *Stylochaeton* and *Jasarum* is an extensive and more or less typical reticulum retained, although certain

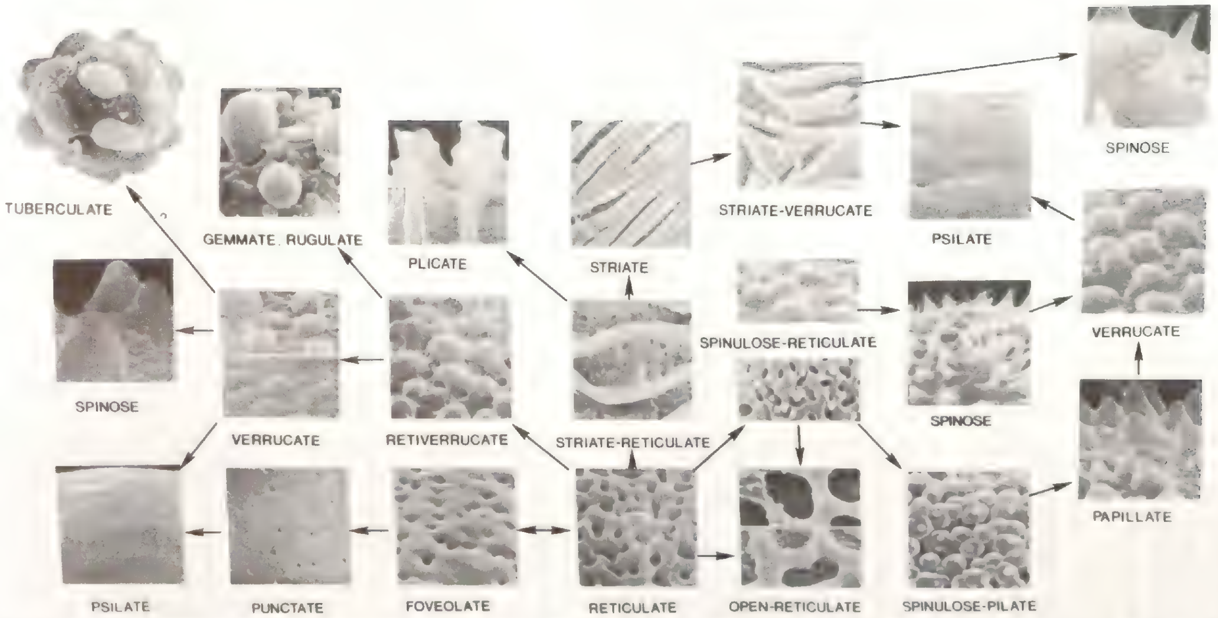


FIGURE 490. Scheme for the evolution of exine sculpturing in the Araceae. Examples are as follows: reticulate = *Dracontioides desciscens*; foveolate = *Calla palustris*; punctate = *Rhodospatha oblongata*; psilate (punctate-derived) = *Philodendron radiatum*; retiverrucate = *Culcasia longevaginata*; gemmate = *Anthurium clidemioides*; verrucate (retiverrucate-derived) = *Asterostigma pavonii* (upper) and *Philodendron rugosum* (lower); spinose (verrucate-derived) = *Synandrospadix vermitoxicus*; tuberculate = *Syngonium standleyanum*; striate-reticulate = *Ambrosina bassii*; plicate = *Pistia stratiotes*; striate = *Protarum sechellarum*; striate-verrucate = *Colocasia indica*; psilate (striate-verrucate-derived) = *Amorphophallus titanum*; spinose (striate-verrucate-derived) = *Colocasia esculenta*; open-reticulate = *Anthurium redolens* (upper) and *Lysichiton camtschatcensis* (lower); spinulose-reticulate = *Pinellia cordata* (upper) and *Anthurium willdenowii* (lower); spinose (spinulose-reticulate-derived) = *Anthurium friedrichsthalii*; verrucate (spinose-derived) = *Typhonium trilobatum*; spinulose-pilate = *Anadendrum montanum*; papillate = *Callopsis volkensii*. Exine sculpturing of the species selected is thought to have evolved in the manner depicted, but not from the other extant taxa in the diagram.

presumably transitional stages occur in other genera, as will be discussed. Indeed, some trace of a foveolate or microreticulate exine structure is apparent in every major inaperturate-grained taxon except Pistioideae: i.e., in *Amorphophallus* (Figs. 368–372) among the inaperturate Lasioideae; in *Dieffenbachia* (Fig. 444) and perhaps *Typhonodorum* (Fig. 476) of the Philodendroideae; in *Jasarum* (Figs. 275, 276), *Xanthosoma* (Fig. 445), *Chlorospatha* (Fig. 455), and *Syngonium* (Fig. 303) of the Colocasioideae; and in *Stylochaeton* (Figs. 446, 456), *Theriophonum* (Fig. 486), *Lazarum, Pinellia* (Fig. 487), *Arisarum* (Fig. 465), and *Ambrosina* (Fig. 466) of the Aroideae.

Foveolate and reticulate (that is, microreticulate in the sense of Praglowski & Punt, 1973) exines being more or less equally common in monosulcate Araceae, it is not clear which of the two subtypes is the more primitive. One of these two exine types is, however, envisioned as the primitive type for Araceae; a double-headed arrow has been used in Figure 490 to suggest their equal likelihood of being ancestral, as well as to indicate the possible interconvertibility of the two forms.

A few additional peculiarities of the basic foveolate-reticulate exine type remain to be considered. Fossil monocot pollen, as well as monosulcate pollen of numerous extant families (see, e.g., Fig. 513), is often characterized by a heterobrochate reticulum in which most of the grain surface has relatively large brochi that become much reduced toward the aperture and/or toward the equatorial "ends" of the grain (Doyle, 1973; Walker & Doyle, 1975). The authors just cited suggested that this type of reticulum is especially primitive. In Araceae, the reticulum size commonly diminishes to a greater or lesser extent in the direction of the aperture in monosulcate as well as zonate pollen; in extreme cases a distinct margo is apparent (see especially Figs. 126, 129, 143, 145, 149, 157). However, a clear reduction in the size of the brochi toward the "ends" of the grain was noted only in *Dracontium polyphyllum* (Fig. 158). A more focused search for this feature in aroid pollen is perhaps indicated.

Another feature of reticulate aroid exines occasionally noted is the presence of what are here interpreted (in the absence of TEM data) as free-standing columellae. These are clearly visible within the brochi in *Gonatopus angustus* (Fig. 449), *Monstera tenuis* (Fig. 89), *Lasia spinosa* (Fig. 453), *Anaphyllum wightii* (Fig. 146), *Pycnospatha arietina* (Fig. 454), and *Stylochaeton zenkeri* (Fig. 456). The significance of this feature in Araceae is not well understood. Also to be noted are the strikingly similar "compound" foveolae or brochi seen in *Dracontium polyphyllum* (Fig. 159), *Dieffenbachia pittieri* (Fig. 444), and *Chlorospatha croatiana* (Fig. 455).

Among the five major evolutionary trends (Fig. 490) envisioned to have proceeded from the basic foveolate-reticulate exine type in Araceae, perhaps the most basic involve simply a decrease or increase in the size of the brochi. The former trend may terminate in psilate exines. Such a trend is most clearly seen in the tribe Monstereae (to a lesser extent in Lasieae, e.g., *Cyrtosperma*). Within *Monstera* the primitive exine type is regarded as that with the larger brochi (e.g., Fig. 89). From this, more and more shallowly and remotely foveolate to punctate exine types (Figs. 91, 93) have been derived, culminating with the appearance of perfectly psilate pollen as seen in *Monstera tuberculata* (Fig. 94).

The other extreme, open-reticulate pollen (or reticulate sensu Praglowski & Punt, 1973), is uncommon in Araceae and consequently is interpreted as a specialized feature. It occurs, for example, in *Lysichiton* (Fig. 128), *Lasia* (Fig. 453), *Pycnospatha* (Fig. 454), and numerous species of *Anthurium* (e.g., Fig. 450). I regard this trend as an evolutionary dead end in Araceae, although by further enlargement and elongation of such an open reticulum, striate pollen of the type seen in *Spathiphyllum* might have been derived, as is discussed later (see Fig. 65).

A third trend begins with the development of minute nubs or spinules along the muri of foveolate-reticulate grains. Pollen in the initial stages of this proposed trend can be seen in *Pothos* sect. *Allopothos* (Figs. 9, 10), and, especially, in many species of *Anthurium* (Figs. 457, 458, and others). Such spinulose-reticulate pollen can undergo enlargement of the brochi and become open-reticulate, as in *Anthurium redolens* (Fig. 459). At the other extreme, enlargement of the spinules accompanied by diminution in the size of the brochi may result in typical spinose pollen. This is clearly the manner in which the spinose pollen of *Anthurium friedrichsthalii* (Fig. 480) must have evolved; indeed, traces of punctae are still visible among the spines in this species. The spinulose and spinose pollen of *Pinellia cordata* (Fig. 487) and *Theriophonum infaustum* (Fig. 486), respectively, also reveal a distinct microreticulate interspinal exine surface and may have evolved through the pathway just described.

A spinulose-pilate exine much like that of pollen of *Anadendrum* (Fig. 472) may be derived from the basic spinulose-reticulate type merely via a partial or complete breakdown of the reticulum, isolating the spinuliferous pilae or baculae. Further spreading and modification of these columns might yield the papillate type of exine seen in *Callopsis* (Fig. 483). From either the papillate or typical spinose exine types, it is probable that verrucate and perhaps ultimately even completely psilate exines may be derived. The verrucate exine of *Typhonium trilobatum* (Fig. 475) probably evolved from the spinose type more prevalent in this genus, rather than vice versa (see Grayum, 1986c).

Returning to the foveolate-reticulate base of Figure 490, a fourth major trend commences with the breakdown of a typical psilate (i.e., nonspinulose) reticulum. In Araceae, the early stages of this trend are seen to best advantage in *Culcasia longevaginata* (Fig. 468), where what are evidently columellae may still be seen supporting what appear to be brief intact segments of the degraded reticulum. Such a condition has been termed "retiverrucate" (by analogy with "retipilate") in this report. The exine of *Rhaphidophora africana* (Fig. 83) exemplifies this same evolutionary stage. Here, the reticulate pattern is almost entirely preserved; however, the "muri" appear to be composed of countless discrete gemmulae or granules.

Also included in the retiverrucate category, though columellae can no longer be detected, is the pollen of *Gorgonidium vargasii* (Fig. 469). The verrucae of this species retain a distinctly reticulate or rosettelike arrangement (light microscopists would have called this type of exine "alveolate"); indeed, this is one of the closest approaches to reticulate exine in the tribe Spathicarpeae (see also Bogner & Nicolson's (1988) SEM micrographs of *Gorgonidium vermicidum* pollen). It is thus of great interest that the pollen of *G. vargasii* is apparently monosulcate or monosulcoidate. It is also tempting to postulate that the subcircular psilate patch frequently seen on pollen of *Culcasia* (Fig. 414) and *Nephthytis* (see Knecht, 1983a) may represent the vestige of an aperture.

Typical retiverrucate and "alveolate" exine types, seen to represent more or less the same evolutionary grade, have probably given rise in most cases to verrucate exine through the disappearance of all "bridges" representing segments of the former reticulum. It is probable that the very rare gemmate type of exine seen only in *Anthurium* sect. *Polyphyllum* (Fig. 473) has been derived from the retiverrucate grade by means of the bulbous enlargement of segments of the former reticulum (with two or more columellar attachments per gemma usually discernible). Rugulate exine, also rare in Araceae (see Fig. 294), may have arisen from the retiverrucate stage via a loss of columellae and the retention of the old reticular segments.

Verrucate exine in Araceae is interpreted here as an intermediate stage from which several other exine types have been derived and through which they may be interconvertible to an extent. On the one hand, verrucae may become rather low and flattened (as in *Philodendron rugosum*, Fig. 203), gradually blending in the evolutionary sense into verruculate or scabrate and, ultimately, perfectly psilate exines. This is considered to be the manner in which psilate exines have generally evolved in *Philodendron* and the Spathicarpeae, for example. In both of these taxa, verrucate or "alveolate" exines are believed to represent the primitive type, although it is not necessarily true that verrucate exine is primitive in every species in which it occurs (i.e., perhaps verrucae can arise secondarily from a psilate exine).

On the other hand, verrucae may become rounded, discrete, and quite conspicuous, as in *Asterostigma pavonii* (Fig. 242), *Gorgonidium mirabile* (Fig. 251), *Philodendron leal-costae* (Fig. 474), and *Syngonium schottianum* (Fig. 291). They may even assume the aspect of spines. The rather blunt spines of *Synandrospadix vermitoxicus* (Fig. 245) of the tribe Spathicarpeae have almost certainly evolved from verrucae, as have also the sharper but sparse and irregularly distributed spines of *Taccarum cardenasianum* (Fig. 249). *Synandrospadix* has the only globose pollen in Spathicarpeae, underscoring the close correlation between spinose exine and globose pollen shape in Araceae; *Taccarum cardenasianum* is the only aroid species known to have boat-shaped, spinose pollen.

A verrucate origin is clearly also indicated for spines on pollen of *Culcasia angolensis* (see Knecht, 1983a), and perhaps in those species of *Syngonium* with spinose pollen. Surprisingly, no spinose pollen is yet known from the basically verrucate-grained genus *Philodendron*.

A final and much more questionable, speculative trend that may proceed from a verrucate precursor leads to the striking tuberculate pollen seen in *Dieffenbachia parlatorei* (Fig. 423), *Syngonium standleyanum* (Fig. 426), and *S. triphyllum*. These peculiar forms need to be studied at the TEM level. The protuberances on this type of pollen are at least an order of magnitude larger than the typical verrucae seen in araceous pollen, and they exhibit a microreticulate exine sculpturing pattern of their own (Figs. 219, 303). This never occurs in more typical verrucae, which are themselves interpreted as vestiges of such a reticulum. Judging from light slides, the protuberances in *Syngonium* and *Dieffenbachia* are not merely sexinous, but rather appear as evaginations involving the whole pollen wall (though there is no sign of continuity between the interior of the protuberances and the grain proper). Perhaps these pollen types have evolved in a saltatory fashion more or less directly from globose, fully reticulate primitive forms. The fact that the only hint of a reticulum in the entire genus *Syngonium* occurs atop these tuberculae favors this possibility.

The fifth major evolutionary trend leading away from the basic foveolate-reticulate exine type in Araceae (Fig. 490) results in striate and striate-derived pollen types. Striate pollen, though known from a range of dicot families, is quite rare in monocots; no palms, for example, are known to have striate pollen (Thanikaimoni, 1970). Outside Araceae, I have been able to find reports of striate pollen in monocots only in *Dioscorea* (Erdtman, 1952) and in *Tripogandra* of the Commelinaceae (Mattson, 1976). The most well-known striate pollen is that of *Ephedra*, which is illustrated in this paper (Figs. 592–595), mainly because it has often been compared to certain aroid types. Trevisan (1980) has, however, shown at the TEM level that the resemblance is quite superficial. In Araceae striate pollen is widespread, occurring in Monsteroideae (Spathiphylleae; see, e.g., Fig. 460), Lasioideae (e.g., *Pseudodracontium*, Fig. 363), Colocasioideae (*Steudnera*, Fig. 461; *Colocasia*, Fig. 462), Aroideae (*Protarum*, Fig. 464; *Arisarum*, Fig. 465; *Ambrosina*, Fig. 466), and Pistioideae (Fig. 467).

The necessary postulation of a connection between reticulate and striate pollen types in Araceae is facilitated by the existence of more or less intermediate striate-reticulate forms in *Arisarum* (Fig. 465), *Ambrosina* (Fig. 466), and in two species of *Amorphophallus* (Figs. 368–372). The reticulum in *Amorphophallus putii* is so large, and the striae are so flat, that at high magnification (Fig. 369) it is difficult to detect the striate pattern. *Arisarum*, with the only aroid pollen having distinctly foveolate striae (Fig. 465), exhibits perhaps the most primitive striate type of all. A similar trend from reticulate to striate-reticulate pollen has been reported in Polemoniaceae (Taylor & Levin, 1975).

Striate-reticulate pollen much like that of *Ambrosina* (Fig. 466) must have been antecedent to the distinctive "plicate" type of pollen of *Pistia* (Fig. 467). Indeed, the exine sculpturing of these two genera differs little except for the complete absence of reticulum in *Pistia* along with the thinner, higher plicae. Particularly striking is the distinct, vertical ribwork running along the plicae and decurrent onto the intervening furrows in both genera (Figs. 466, 467).

Amorphophallus is the most eurypalynous genus in the Araceae, comprising, in addition to striate pollen, psilate, verrucate, and even spinose types. The status of striate pollen as the most primitive type in this genus is strongly supported by the fact that this is the only type showing evidence of a reticulum. In addition, boat-shaped pollen in *Amorphophallus* is almost exclusively associated with striate exine sculpturing (only two psilate-grained species have boat-shaped pollen). The mean size of striate pollen in *Amorphophallus* (46 μm) is considerably smaller than that of nonstriate pollen (61 μm), and thus much closer to the putatively primitive condition for Araceae. Furthermore, *A. longituberosus*—one of the species with striate-reticulate pollen—has an elongate subrhizomatous rootstock, perhaps a primitive condition in this largely tuberous genus.

The evolution of the more derived exine types from striate-reticulate pollen in *Amorphophallus* probably occurred according to the following scenario. Boat-shaped, striate-reticulate pollen such as that of *A. longituberosus* (Figs. 370–372) gave rise via a closure of the reticulum to boat-shaped, simply striate pollen such as that of *A. kerrii* (Figs. 373–375) and eventually to globose, striate pollen (e.g., that of *A. corrugatus*, Figs. 376, 377). This much is easy enough to grasp, but from here to psilate or verrucate pollen seems a big leap. A key intermediate may be pollen such as that of *Amorphophallus konjac* (Figs. 378, 379); though still retaining clear evidence of a striate derivation, pollen of this type may have evolved into perfectly psilate pollen (e.g., that of *A. titanum*, Figs. 386, 387) via a closure of the furrows, or into verrucate pollen (e.g., that of *A. schweinfurthii*, Figs. 380, 381) by a widening of the furrows at the expense of the intervening platelike regions. From verrucate to spinose pollen, as in *A. flavovirens* (Figs. 382, 383), would seem a simple step, analogous (though probably not homologous, as will be seen later) to the origin of spines in *Synandrospadix* discussed previously.

Evidence of these trends can be seen in other aroid taxa. The pollen of *Scaphispatha gracilis* (Figs. 277, 278), which is unique among Araceae in its polygonal verrucae, may be on this same evolutionary pathway, though it appears to be more to the verrucate side of *Amorphophallus konjac*. Pollen at roughly the same striate-verrucate evolutionary grade as *A. konjac* also occurs in *Coloca-*

sia indica (Figs. 310, 311), only in this species it is even more evidently striate. The small genus *Colocasia* (assuming it is a natural assemblage) succinctly exemplifies in the three species examined the entire evolutionary history of the derivation of spherical, spinose pollen from boat-shaped, striate pollen via an ellipsoid, striate-verrucate intermediate (Figs. 308–313). Even the spherical, spinose pollen of *Colocasia esculenta* appears to exhibit traces of a striate pattern, there being shallow channels or furrows evident between the spines (Fig. 484). Presumably the spines originated as de novo structures, there being no sign of verrucae in this admittedly incomplete series. Significantly, all three of these radically different pollen types in *Colocasia* are within a micrometer of the exact same size.

It is almost certain that striate pollen has evolved at least twice in Araceae: once in the Spathiphylleae, and at least one other time. If the Colocasioideae do indeed represent a monophyletic line, contrary to recent evidence (French et al., 1992), then it must be supposed that striate pollen evolved independently here (in the Old World genera) as well.

The totality of nonpalynological characters virtually dictates an independent origin of striate pollen in the tribe Spathiphylleae. Indeed, there may be a fundamental difference in the structure of the striae between pollen of this group and other striate-grained Araceae. According to Trevisan (1980) the striae of *Spathiphyllum* are tectate and columellate. Lugardon et al. (1988) confirmed that the tectal and infratectal layers are restricted to the striae in *Spathiphyllum*. Perhaps the striae in Spathiphylleae represent single muri of a reticulum that has become greatly enlarged and drawn out. The presence of foveolate striae in pollen of *Arisarum* as well as the clearly polybrochate furrows in this genus, *Ambrosina*, and certain species of *Amorphophallus* suggest a more complicated derivation of striae in these genera.

Summarizing the conclusions on the evolution of exine sculpturing in Araceae: the basic foveolate to reticulate exine type is thought to have given rise to punctate, verrucate, striate, and spinulose-reticulate exines, all thought to represent more or less intermediate evolutionary grades. Note that striate pollen, though virtually limited to Araceae among monocots, is not considered particularly advanced within Araceae. The most highly advanced common exine types in Araceae are the psilate and spinose types. As might be expected, each of these types may have evolved in any of several different ways, and they represent the end points of most major evolutionary pathways. Each has been shown to be correlated closely with a highly specialized pollination mode (Grayum, 1986c). Spinose exine occurs almost exclusively on spherical pollen, likewise an advanced condition; in Araceae only *Taccarum cardenasianum* (Fig. 419) is known to have boat-shaped, spinose pollen.

The concept of psilate exine as a derived condition in Araceae is at variance with some previous evaluations for other taxa; nonetheless, van der Ham (1990) recently arrived at a similar conclusion in his superbly detailed palynological study of Sapindaceae tribe Nephelieae.

Apertural exine. No Araceae are known to have compound or operculate apertures, as seen, for example, in some Philydraceae (Fig. 551), palms (Figs. 503, 508), and lilialean families (Roth et al., 1987). The nature of the aperture membrane in Araceae may be difficult to ascertain unless absolutely fresh material is used. In a few species, e.g., *Symplocarpus foetidus* (Figs. 131, 132), *Calla palustris* (Fig. 136), and *Rhaphidophora reineckei*, the aperture membrane is coarsely and conspicuously verrucate. In *Anthurium margaricarpum* the pores are spinulose as in *Alisma* (Fig. 582). Mostly, the apertural membrane appears obscurely verruculate or psilate, but frequently it cannot be seen at all due to the material.

Thanikaimoni (1970) believed psilate aperture membranes to be primitive in palms, and perhaps this is also true for Araceae; at any rate, it seems likely that the more coarsely verrucate and spinulose types represent specializations. Further analysis must await a thorough study of aperturate aroid pollen utilizing absolutely fresh material.

EXINE STRUCTURE IN ARACEAE

Although exine structure was not directly investigated in the present work, some speculations and predictions can be made based on the scheme for the evolution of exine types already presented (see Fig. 490). Information on exine structure is available in the literature for only a handful of aroid genera, viz., *Anthurium* and *Zamioculcas* (Tarasevich, 1989), *Spathiphyllum* and *Holochlamys* (Trevisan, 1980; Lugardon et al., 1988), *Lysichiton* (Hesse, 1980), *Cyrtosperma* (Van Campo & Lugardon, 1973), *Arum* (Hesse, 1980), and *Arisaema* (Zavada, 1983; Ohashi et al., 1983; Oh et al., 1990). Critical data from these sources have been integrated into the following account, employing the terminology of Walker (1976).

Exine thickness in araceous pollen was measured from light slides, but these data were not quantitatively analyzed since it can be difficult to ascertain the limits of the exine; moreover, exine thickness varies greatly within a single grain. Sowunmi (1972) reported that exine thickness in palms ranges from 0.8 to 6.3 μm, with most genera falling into the 1–3 μm range. This states the case for Araceae remarkably well. Unusually thick exines (i.e., more than 3 μm) occur in Zamioculcadeae, *Cyrtosperma*, Cryptocoryninae, Spathicarpeae, a few *Amorphophallus* species (especially *A. flavovirens*), and *Arisarum*. Exines of such thickness were not observed in any other monocot species examined in this study and are presumed to have been derived in the above taxa—no doubt many times, as the list is taxonomically diverse and also includes all aperture and exine types, and a range of shapes and sizes. Especially thin and delicate exines, as seen in *Montrichardia* and the Nephthytideae, probably also represent a derived condition.

The basic evolutionary scheme for internal exine structure here proposed for Araceae conforms in essence to the schemes proposed for angiosperms and monocots as a whole by Walker (1976) and Zavada (1983), respectively. The same trend was postulated by Chanda et al. (1988) for Alismatales. The most primitive exine structure for Araceae, as for monocots in general, is seen to be tectate-perforate with a columellate interstitium (see Walker & Walker (1981) for a definition of the latter term). This condition is most typical of aroids with aperturate pollen and differs only by degree from the semitectate (i.e., open-reticulate) type of exine also seen in these taxa.

The occurrence of apparent free-standing columellae in several aroid genera has already been discussed; in addition, typical attached columellae can occasionally be seen on SEM micrographs, especially on grains with a fairly large reticulum as in some *Anthurium* species (Fig. 459). At the TEM level, Tarasevich (1989) confirmed the tectate-columellate nature of *Anthurium* pollen, as well as *Acorus* and *Zamioculcas*, and Hesse (1980) described "short columellae" in pollen of *Lysichiton*; however, the latter interpretation was questioned by Zavada (1983). In the inaperturate, striate pollen of *Spathiphyllum*, columellae are clearly visible on SEM micrographs at the base of the striae (Fig. 460). Trevisan (1980) had reported a columellate structure for *Spathiphyllum* exine at the TEM level; however, Lugardon et al. (1988) described a granular interstitium in both *Spathiphyllum* and *Holochlamys*. It is possible that this pollen should, in addition, be considered semitectate, i.e., with the striae representing enlarged muri, and the furrows corresponding to enlarged and drawn out brochi of a reticulum. The other alternative is that the so-called columellae may represent merely the reduced vestiges, e.g., muri, of a former reticulum as, for example, in *Ambrosina* (Fig. 466); in this case, *Spathiphyllum* pollen might best be described as tectate-semiperforate.

Pollen types resulting from the stricture and ultimately even the closure of brochi (tectal perforations), as seen in the tribe Monstereae, remain tectate, but in the extreme case (e.g., the perfectly psilate pollen of *Monstera tuberculata*) ought to be tectate-imperforate—secondarily so, since this condition is envisioned as primitive for columellate angiosperm pollen (Walker, 1976). This trend ought to hold up also for spinose, verrucate, and psilate pollen derived from the reduction and ultimate closure of a spinulose reticulum. If the hypotheses proposed here are correct, then exine structure in species such as *Pinellia cordata* (Fig. 487), *Theriophonum infaustum* (Fig. 486), and some *Anthurium* species should be tectate-perforate. On the other hand, exine structure of nonfoveolate spinose and verrucate pollen types derived via this pathway (presumably the entire Arinae (Figs. 333–353) plus perhaps *Arisaema* (Figs. 354–356) and *Ariopsis* (Figs. 357, 358)) should be tectate-imperforate. Note that all exine ornamentation, spines, verrucae, etc., is expected to be supratectal in the above genera. The literature is not illuminating with regard to these taxa; Hesse (1980) described pollen of *Arum maculatum* as "without a tectum"; however, Zavada (1983) indicated that pollen of *Arisaema triphyllum* is indeed tectate-imperforate. Ohashi et al. (1983) and Oh et al. (1990), on the other hand, reported all 32 species of *Arisaema* studied by them to be intectate. These discrepancies are no doubt due to confusion regarding terminology rather than to actual interspecific morphological differences.

The situation in striate aroid pollen, apart from Spathiphylleae, is less clear. All striate and striate-derived pollen types in Araceae may be tectate (based on the observation of foveolate striae in *Arisarum*) and for the most part imperforate. No pollen of this type has ever been examined by TEM.

Probably relatively few tectate araceous pollen types retain a columellate interstitium. Walker (1976) stated that "there is convincing evidence that secondarily tectate-imperforate pollen in angiosperms may lose its columellar structure and become secondarily granular" (secondarily, inasmuch as a granular interstitium is considered to precede the columellate type for angiosperms). Such a trend was also postulated for monocots by Zavada (1983). The nature of the interstitium in the open-reticulate exine of *Lysichiton* is already ambiguous, as discussed previously; in the monosulcate, presumably tectate-perforate pollen of *Cyrtosperma hastatum,* Van Campo & Lugardon (1973) described the interstitium as granular. Thus the interstitium in all tectate-imperforate aroid pollen is most likely granular, as reported for *Arisaema triphyllum* (Zavada, 1983), or perhaps even secondarily atectate (or, better, "noninterstitiate" (Walker & Walker, 1981))—secondarily, since this is usually regarded as the most primitive condition in angiosperms (Walker, 1976). Guédès (1982), however, believed angiosperm pollen to be primitively columellate.

Exine types in Araceae considered to be derived from the breakdown of the basic reticulate structure should prove to be partially or completely without a tectum, if the hypotheses presented here are correct. So-called retiverrucate exine, in which intact segments of a reticulum may still be discerned (as in *Culcasia longevaginata,* Fig. 468), appears intermediate between semitectate exine, in which the reticulum is more or less complete, and intectate exine, in which the reticulate structure, but not necessarily the pattern, is obscured. It is suggested here that the word "distectate" be employed for exines at this early stage of tectal degradation. This term may also be applied to gemmate and rugulate exines in Araceae.

In cases where intact segments of reticular muri are no longer discernible and the vestiges of a tectum are limited to more or less isolated pilae, papillae, verrucae, or spines, the term "intectate" is indicated. This should prove to be the situation, for example, in the spinulose-pilate pollen of *Anadendrum* (Fig. 472), as well as in verrucate and spinose pollen of *Philodendron* and the tribe Spathicarpeae. The existence of intectate exines has also been proposed for palms; Sowunmi (1972) stated that about 11.5% of palm pollen is apparently intectate.

Walker (1976) coined the term "etectate" to describe pollen "that appears to be derived from intectate pollen and which possesses an exine that consists only of a nexine-like layer with no sexine," while observing at the same time that he did not know of any actual examples. If the present conception of the evolution of exine types in Araceae is substantially correct, then certain psilate aroid pollen types, e.g., in *Philodendron* and the tribe Spathicarpeae, should prove to be etectate. This is conceivable in the relatively thin-walled grains of *Philodendron* and the Nephthytideae, for example. In thick-walled pollen of groups such as Spathicarpeae and Cryptocoryninae, however, the nexine would have to have thickened. This is perhaps not farfetched, as even the intine may be thickened in some very thin-walled grains (Zavada, 1983), including *Montrichardia* in the Araceae (Thanikaimoni, 1969). In any case, it is difficult to imagine how one would distinguish etectate from psilate, atectate (noninterstitiate) exine even at the TEM level, and the same applies to intectate versus spinose (or verrucate, etc.) atectate exine. Thus, in the long run, inferences drawn from comparative SEM studies may have to be applied in the interpretation of TEM micrographs in certain cases, rather than the other way around.

In summary, the evolution of pollen exine structure in Araceae as extrapolated from the scheme developed for the evolution of exine sculpturing types (Fig. 490) is perceived to correspond with Walker's (1976) fig. 5 (ignoring the most basal stage), drawn up for the angiosperms as a whole, noting only the interposition of the proposed "distectate" stage between the semi- and intectate levels. Aroid pollen exhibiting similar exine sculpturing but derived via different pathways in theory ought to be distinguishable with TEM studies in many cases. Thus psilate pollen may be either tectate-imperforate, etectate, or perhaps even noninterstitiate. Spinose or verrucate pollen may be tectate-perforate or -imperforate, distectate or intectate or possibly noninterstitiate as well. TEM studies in taxa for which the evolutionary origin of exine sculpturing is less certain, e.g., Arophyteae and the New World Colocasioideae, may help to clear up their phylogenetic relationships.

The columellate type of interstitium, though held to be primitive in Araceae, is probably of restricted occurrence. Columellae appear practically limited to genera with aperturate pollen, and even some monosulcate grains are reputed to have a granular interstitium. The latter is expected to be the most widespread type in Araceae, reported from such taxonomically disparate genera as *Cyrtosperma* and *Arisaema.* Secondarily noninterstitiate exine, though not definitely reported from Araceae, may also occur.

Among Araceae with inaperturate pollen, columellae are reported only in *Spathiphyllum* (Trevisan, 1980; cf. also *Stylochaeton*). If the striae of *Spathiphyllum* are indeed truly columellate (Lugardon et al., 1988, described a granular infratectal layer in this genus), then a radically different mode of origin is indicated for the striate exine pattern of this pollen: e.g., by means of expansion and "stretching" of an open reticulum, the muri of which must correspond to the striae themselves (the furrows would then represent single brochi, and be floored with nexine). Striation in genera such as *Amorphophallus*, *Arisarum*, *Ambrosina*, and *Pistia* may have evolved through reduction rather than an expansion of the basic foveolate-reticulate exine pattern. The striae appear to represent tectal folds that involve whole strips of reticulum, or else series of individual muri that have become linearly oriented, whereas the furrows are envisioned as polybrochate and wholly sexinous. Thus, *Spathiphyllum* pollen is perhaps semitectate, whereas that of other striate-grained aroids appears to be tectate-imperforate or -perforate.

EXINE STRATIFICATION

Endexine has been sought in only five genera of Araceae, so far as I am aware. Van Campo & Lugardon (1973) reported endexine in pollen of *Cyrtosperma*, and Trevisan (1980) and Lugardon et al. (1988) in that of *Spathiphyllum*. Chanda & Rowley (1967) spoke of "nexine 1" and "nexine 2" in TEM sections through the germinal aperture of an unidentified *Anthurium* species, the latter of which is evidently equivalent to endexine. Tarasevich (1989) confirmed the presence of endexine in numerous *Anthurium* species, and also reported it in *Zamioculcas* (he apparently did not find an endexine layer in pollen of *Acorus*). Ohashi et al. (1983), from their extensive TEM and SEM study of 28 Japanese species of *Arisaema*, described as characteristic a "thin ektexine with two-layered membrane" and an endexine that is "almost uniformly thick and appears to be a loose texture associated with granular materials and inclusions of less stainability." Evidently, the same layer that Ohashi and coworkers labeled "endexine" has been interpreted as a granular interstitium by Zavada (1983), who reported no endexine in pollen of *Arisaema triphyllum*, and attributed the same conclusion to Hesse (1980) regarding pollen of *Lysichiton americanus* and *Arum maculatum*. Actually, Hesse did not address the matter at all, hence the alleged lack of endexine in these genera apparently rests on Zavada's interpretation of Hesse's published TEM micrographs. Recently, Oh et al. (1990) have seconded the interpretation of Ohashi et al. (1983). Nonetheless, as reasoned in the previous section, I suspect Zavada's analysis to be correct.

Endexine is very rare in monocots, and when present is quite different from the endexine of dicots in that it is "spongy" and does not become thickened in the aperture region (Zavada, 1983). Indeed, Zavada spoke of the "proposed monocotyledonous endexine." Apart from Araceae, he cited positive reports of endexine in Rapateaceae, Mayacaceae, Dioscoreaceae, and *Zea*, and dubious reports in Hydrocharitaceae, Juncaginaceae, and Scheuchzeriaceae. More recently, Simpson (1985b) reported endexine in the Tecophilaeaceae. Regardless of whether monocot endexine is homologous with dicot endexine, its distribution may prove to be a useful taxonomic character and should be researched more extensively.

SOME TAXONOMIC IMPLICATIONS OF POLLEN CHARACTERS IN ARACEAE

For the purposes of the phylogenetic analysis of Araceae conducted in conjunction with this study (see Grayum, 1990), pollen characters were accorded no special significance. Rather, an attempt was made to consider characters from all fields without bias. Nonetheless, in certain cases pollen characters provide especially important insights. Some of the more noteworthy conclusions or implications emerging from the present study are enumerated below. Data on pollen starch content and nuclear number are from Grayum (1985, 1986a).

1. The identical pollen morphology of *Pothos* sect. *Allopothos* and *Pedicellarum* suggests a close relationship between these taxa.
2. The rather large, zonate, starchy, binucleate pollen grains of *Zamioculcas* and *Gonatopus* strongly support a close relationship between these genera and point to their inclusion in subfamily Monsteroideae.
3. The inaperturate, starchy pollen of *Culcasia* supports its removal from the Pothoideae, and exine sculpturing suggests a relationship with *Nephthytis* and allied genera.
4. The spinulose-reticulate exine common in *Anthurium* indicates a relationship with *Pothos*. The inaperturate, gemmate pollen of *Anthurium* sect. *Polyphyllium* is unique within the genus and invites a reconsideration of the status of this section.
5. The zonate, starchy pollen of at least some *Heteropsis* species, and the discovery of dicolpate pollen in *Rhaphidophora*, argue for inclusion of *Heteropsis* within the Monsteroideae.
6. Pollen morphology offers conclusive support that there are indeed two species of *Peltandra*; pollen morphology appears promising at the species level in several other genera, no-

tably *Epipremnum, Dieffenbachia, Syngonium, Colocasia, Typhonium,* and *Amorphophallus.*

7. The isolated status of *Philodendron goeldii* and *P. leal-costae,* alone in the genus in their possession of pedately compound leaves, is reflected in pollen morphology.
8. Pollen morphology strongly supports the removal of *Bognera* from near *Ulearum* to near *Dieffenbachia.*
9. Pollen morphology and other characters suggest that *Ulearum* and *Filarum* are closely related, and that *Zomicarpa* stands apart.
10. *Anchomanes nigritianus* and *Pseudohydrosme gabunensis* share a unique type of very large, oblong pollen that underscores the proposed relationship between the two genera; the inaperturate, psilate, starchy, binucleate pollen suggests that the genera belong in subfamily Philodendroideae.
11. That subfamily Colocasioideae may be diphyletic is suggested by the fact that the Old World genera have basically striate exine, while exine of the New World genera is primitively reticulate (see Grayum, 1990: 769–680).
12. Pollen of *Aphyllarum* is borne in monads, which is consistent with the recent merger of that genus with *Caladium.*
13. *Xanthosoma* and *Chlorospatha,* though both shedding pollen in tetrads, may be distinguished on the basis of pollen size and starch content, and perhaps nuclear number.
14. Pollen morphology points toward submerging *Gonatanthus* in *Remusatia,* as recently effected by Li & Hay (1992).
15. Pollen morphology is inimical to a proposed merger of *Dracunculus* and *Helicodiceros.*
16. The inaperturate, starchy, trinucleate pollen prevailing in tribe Thomsonieae argues strongly for the dissociation of this group from the Lasieae, and supports placement near subtribe Arinae (Grayum, 1990; Bogner & Nicolson, 1991).
17. The integrity of *Pseudodracontium* is confirmed by its consistently distinctive pollen morphology.
18. The small size and peculiarly striate exine sculpturing of *Protarum* appear to link this genus to *Steudnera* of the Colocasioideae.
19. The striking overall similarity of *Pistia* pollen to that of *Ambrosina* vindicates earlier conclusions proposed on the basis of floral morphology (see e.g., Buscalioni & Lanza, 1935) that these genera are next of kin. At the same time, the commonly assumed relationship of *Pistia* with the Lemnaceae is countervailed.

PART 2. EXTERNAL POLLEN MORPHOLOGY OF AROID OUTGROUPS

A brief SEM survey was undertaken of external pollen morphology for representative species of 21 families postulated at one time or another as close relatives of the Araceae (see Grayum, 1984), using the same methods discussed in Part 1. Approximately 79 species in 58 genera were studied. For larger families, such as the palms, an effort was made to concentrate on a sampling of putatively primitive genera. The results of this survey are depicted in Figures 491–595 and summarized in this section. Pollen of some of these genera has never before been illustrated with scanning electron micrographs.

The data are presented in the formal pollen descriptions exactly as for the Araceae, except that a taxonomic reference has not been cited in every case, and no rigorous attempt was made to account for previously published SEM and TEM micrographs.

SUMMARY OF DATA: DESCRIPTIONS OF EXTERNAL POLLEN MORPHOLOGY IN PUTATIVE AROID RELATIVES

Family: Lemnaceae Figures 491–498.

Taxonomic Reference: Landolt, 1986.

Species/Genera Examined: 12/4 (*Lemna, Spirodela, Wolffia, Wolffiella*).

POLLEN TYPE: *aperture type* ulcerate; *polarity* apolar.
POLLEN SHAPE spherical or subspheroidal; *symmetry* ra-
diosymmetric. POLLEN-UNIT monads. POLLEN SIZE small;
mean *19 μm, range *13 (*Lemna minor*)–46 (*L. tri-*
sulca) μm; generic means: *Lemna* *22 μm, *Spirodela*
*18 μm, *Wolffia* *18 μm, *Wolffiella* *17 μm. *Lemna*
trisulca has by far the largest pollen measured in the
family (even accounting for the fact that it was the only
species measured under light microscopy); no other spe-
cies surpassed 21 μm. EXINE SCULPTURING: *nonapertural*
exine spinulose to spinose, the spines shorter, stouter, and
more numerous in subfamily Wolffioideae (*Wolffia* and
Wolffiella) than in subfamily Lemnoideae (*Lemna* and
Spirodela); interspinal exine virtually psilate (*Wolffia ar-*
rhiza) to minutely (*Wolffia brasiliensis*) or plainly (*Lem-*
na valdiviana) verruculate, usually minutely and/or re-
motely punctate, occasionally (*Wolffiella lingulata, Lemna*
trisulca) punctate-foveolate; *apertural exine* psilate to
minutely verruculate.

REMARKS: See "Remarks" under *Pistia.* The pollen of *Spirodela,* thought to represent the closest link to *Pistia* (e.g., Maheshwari & Maheshwari, 1963), is most relevant in this context. See Landolt

(1986) for additional SEM micrographs and a full discussion of pollen characters in Lemnaceae.

Specimens Examined: Lemna aequinoctialis Welw. (**PS-245**), *Kiener 24866* (MASS), Nebraska. *L. disperma* Hegelm. (PS-463), cult. RUEB (Acc. No. 7190; orig. Australia). *L. minor* L. (PS-466), cult. RUEB (Acc. No. 7766; orig. New Zealand). *L. perpusilla* Torrey (PS-246), *Ahles & McCrary 58805* (MASS), North Carolina. *L. trisulca* L. (**PS-256**), cult. RUEB (Acc. No. 7579; orig. Ontario). *L. valdiviana* Philippi (PS-257), cult. RUEB (Acc. No. 7116; orig. North Carolina). *Spirodela punctata* (G. Meyer) C. Thompson (**PS-258**), cult. RUEB (Acc. No. 7624; orig. Israel). *Wolffia angusta* Landolt (PS-259), cult. RUEB (Acc. No. 7476; orig. Australia). *W. arrhiza* L. (PS-260), cult. RUEB (Acc. No. 7452; orig. Angola). *W. brasiliensis* Wedd. (**PS-169**), leg. B. Havis, Massachusetts; (PS-261), cult. RUEB (Acc. No. 7104; orig. Illinois); (PS-262), cult. RUEB (Acc. No. 7105; orig. Texas); (PS-263), cult. RUEB (Acc. No. 7150; orig. Texas); (PS-264), cult. RUEB (Acc. No. 7306a; orig. Mexico). *W. microscopica* (Griffith) Kurz (PS-468), cult. RUEB (Acc. No. 8359; orig. India). *Wolffiella lingulata* (Hegelm.) Hegelm. (PS-265), cult. RUEB (Acc. No. 7289; orig. Brazil).

Order: Typhales Figures 499–502.

Species/Genera Examined: 2/2 (*Sparganium, Typha*).

POLLEN TYPE: *aperture type* monoulcerate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads (in species examined; see "Remarks"). POLLEN SIZE medium-sized; mean 33 μm, range 29 (*Sparganium*)–37 (*Typha*) μm. EXINE SCULPTURING: *nonapertural exine* rugulate-reticulate, the muri psilate; *apertural exine* rugulate in *Typha*.

REMARKS: *Sparganium eurycarpum* was chosen since it shares a rust fungus with *Acorus*, and was considered by Savile (1979) as the most likely near relative of that genus.

Some species of *Typha* bear pollen in tetrads, as depicted in Punt (1976) and numerous other references.

Specimens Examined: Sparganium eurycarpum Engelm. (**PS-106**), *Markert 53749* (MASS), Massachusetts. *Typha angustifolia* L. (**PS-306**), *Cross & Cross s.n.* (MASS), Massachusetts.

Family: Arecaceae Figures 503–519.

Taxonomic Reference: Uhl & Dransfield, 1987.

Species/Genera Examined: subfamily Coryphoideae 7/7 (*Chamaerops, Chelyocarpus, Cryosophila, Itaya, Rhapidophyllum, Trachycarpus, Trithrinax*); subfamily Phoenicoideae 3/1 (*Phoenix*); subfamily Nypoideae 1/1 (*Nypa*); subfamily Caryotoideae 3/3 (*Caryota, Didymosperma, Wallichia*).

POLLEN TYPE: *aperture type* monosulcate in all species examined except *Nypa*, which is zonate, and *Cryosophila*, in which most grains are trichotomosulcate (but a few are monosulcate). The aperture is clearly operculate in *Chamaerops* and *Rhapidophyllum*; *polarity* heteropolar; subisopolar in *Nypa*. POLLEN SHAPE boat-shaped-oblong in most species, occasionally boat-shaped-elliptic (*Rhapidophyllum*) or -elongate (*Chelyocarpus*); hamburger-shaped in *Nypa*; *symmetry* bilateral or (*Nypa*) isobisymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 34 μm, range 25 (*Phoenix*)–58 (*Nypa*) μm; subfamily means: Coryphoideae 32 μm (range 28–38 μm); Phoenicoideae 25 μm (range 22–29 μm); Nypoideae 58 μm; Caryotoideae 29 μm (range 25–33 μm). EXINE SCULPTURING: *nonapertural exine* Coryphoideae: most genera foveolate; *Cryosophila* foveolate-rugulate; *Chamaerops* subreticulate, the muri psilate. Phoenicoideae: foveolate or foveolate-fossulate, the foveolae reduced or obsolete toward the aperture. Nypoideae: spinose with long, slender, pointed and also short, stout, blunt spines; interspinal exine densely foveolate. Caryotoideae: gemmate (*Caryota*), or retigemmulate and spinulose (*Didymosperma*) or spinose (*Wallichia*); *apertural exine* psilate or subverruculate, where seen. EXINE STRATIFICATION—according to Thanikaimoni (1970), endexine is rare in palms.

REMARKS: A selection of the palm genera considered by Uhl & Dransfield (1987) to be the most primitive was examined, since it was not possible to fully inventory the large palm family. All of these belong to the subfamily Coryphoideae except *Nypa* (Nypoideae) and *Phoenix* (Phoenicoideae). Some authors (e.g., Corner, 1966; Low, 1976) believe caryotoid palms to be most primitive; pollen of three genera in this subfamily was examined in this study, but was found to be quite specialized and hence is not illustrated.

The most unspecialized pollen examined is that of the Phoenicoideae and some Coryphoideae. *Nypa* and the caryotoids have obvious specializations; the Coryphoideae show tendencies toward operculate or trichotomosulcate conditions, neither of which is known from Araceae. See Dransfield et al. (1990) and Harley (1990) for additional SEM micrographs of coryphoid palm pollen, as well as other relevant data and interpretations.

Specimens Examined: Caryota mitis Lour. (PS-350), *How 71933* (A/GH), Hainan. *Chamaerops humilis* L. (**PS-343**), *Ross 291* (A/GH), Sicily. *Chelyocarpus ulei* Dammer (**PS-480**), *Moore & Salazar 9494* (BH), Peru. *Cryosophila nana* (Kunth) Blume (**PS-346**), *Langlasse 820* (A/GH), Mexico. *Didymosperma caudatum* H. A. Wendl. & Drude (PS-352), *Poilane 6101* (A/GH), Vietnam. *Itaya amicorum* H. Moore (**PS-481**), *Moore et al. 9509* (BH), Peru. *Nypa fruticans* Thunb. (PS-482), *Moore 5846* (BH), cult. Florida. *Phoenix acaulis* Ham. (**PS-348**), *Mooney 3774* (A/GH), India. *P. dactylifera* L. (**PS-349**), *Alcott s.n.* (A/GH), Egypt. *P. hanceana* Naudin (**PS-347**), *Wilson 9848* (A/GH), Formosa. *Rhapidophyllum hystrix* (Fraser) H. A. Wendl. (**PS-344**), *Ray et al. 10874* (A/GH), Florida. *Trachycarpus fortunei* (Hook. f.) H. A. Wendl. (**PS-345**), *Forrest 21168* (A/GH), Yunnan. *Trithrinax campestris* Drude

& Griseb. (**PS-483**), *Bartlett 20154* (BH), Argentina. *Wallichia oblongifolia* Griffith (PS-353), *Hooker s.n.* (A/GH), Sikkim.

Family: Cyclanthaceae Figures 520–527.

Taxonomic Reference: Harling, 1958.

Species/Genera Examined: 5/5 (*Asplundia, Chorigyne, Cyclanthus, Evodianthus, Ludovia*).

POLLEN TYPE: *aperture type* monosulcate (*Ludovia*) or, more typically, monoulcerate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small to medium-sized; mean 26 μm, range 19 (*Evodianthus*)–39 (*Cyclanthus*) μm; subfamily Carludovicoideae (i.e., exclusive of *Cyclanthus*): mean 23 μm, range 19–32 μm. EXINE SCULPTURING: *nonapertural exine* almost perfectly psilate (*Evodianthus*) to shallowly and densely (*Cyclanthus*) or remotely (*Chorigyne*) punctate-foveolate, to conspicuously foveolate (*Ludovia, Asplundia*); *apertural exine* psilate to obscurely or distinctly (*Cyclanthus*) verrucate.

REMARKS: *Cyclanthus* belongs in a monotypic subfamily, and is remote from the remaining genera; *Ludovia* and *Chorigyne* differ from the other genera examined here in possessing distichous leaves (and *Ludovia* also in having simple leaves). Clearly, the most primitive pollen examined is that of *Ludovia*.

Specimens Examined: Asplundia sleeperae Grayum & Hammel (**PS-105**), *Grayum 2791* (DUKE), Costa Rica. *Chorigyne pendula* (Hammel) Eriksson (**PS-1161**), *Hammel 9528* (DUKE), Costa Rica. *Cyclanthus bipartitus* Poit. (**PS-432**), leg. J. H. Beach, Costa Rica. *Evodianthus funifer* (Poit.) Lindman (**PS-117**), *Hammel 8011* (DUKE), Costa Rica. *Ludovia integrifolia* (Woodson) Harling (**PS-108**), *Hammel 8205* (DUKE), Costa Rica.

Family: Pandanaceae Figures 528–535.

Taxonomic Reference: Stone, 1972.

Species/Genera Examined: 5/3 (*Freycinetia, Pandanus, Sararanga*).

POLLEN TYPE: *aperture type* monoulcerate or perhaps inaperturate (*Pandanus, Sararanga*); *polarity* heteropolar and perhaps subisopolar (*Sararanga*) to apolar (*Pandanus*). POLLEN SHAPE boat-shaped-elliptic to -oblong; also spherical (*Pandanus*); *symmetry* bilateral to perhaps radiosymmetric (*Pandanus*). POLLEN-UNIT monads. POLLEN SIZE small; mean 33 μm, range 21 (*Pandanus*)–24 (*Freycinetia*) μm. EXINE SCULPTURING: *nonapertural exine* virtually psilate to shallowly punctate-foveolate (*Freycinetia*) to openly reticulate (*Sararanga*) or spinose (*Pandanus*), with the interspinal surface minutely verruculate. Pollen of *Freycinetia* species exhibits a median keel on what is clearly the proximal face (i.e., opposite the aperture); *apertural exine* psilate where seen.

REMARKS: According to Stone (1972), *Pandanus* and *Sararanga* are more primitive than *Freycinetia*. There is no consensus on what sections of the huge genus *Pandanus* are most primitive, hence no guidelines for sampling the genus on a small scale. The species selected has spherical, spinose pollen, but there is considerable variability within the genus; other species have clearly ulcerate, boat-shaped spineless pollen ranging from foveolate to verrucate (Huynh, 1981; Huynh & Stone, 1981). Pollen grains of *Sararanga* and the single *Pandanus* species examined appear inaperturate in the material at hand, but it is probable that they have a tiny, inconspicuous pore as reported by Erdtman (1952). Pollen grains of *Sararanga sinuosa* portrayed at the SEM level by North & Willis (1971) appear to be uniporate.

Pollen of the Pandanaceae does not ever approximate primitive araceous pollen closely, but it does sometimes recall that of certain Cyclanthaceae (see Erdtman, 1952).

Freycinetia marginata Blume is the correct name for *F. australiensis* (Stone, 1982).

Specimens Examined: Freycinetia australiensis Warb. (**PS-356**), *Brass 23859* (A/GH), Papua New Guinea. *F. excelsa* F. Muell. (**PS-357**) *van Royen & Sleumer 6126* (A/GH), W. Irian. *Pandanus pyriformis* (Martelli) H. St. John (**PS-476**) A/GH, *A. C. Smith et al. 16866* (MASS), Fiji. *Sararanga sinuosa* Hemsley (**PS-355**), *Corner 2699* (A/GH), Solomon Islands.

Tribe: Aspidistreae (Convallariaceae) Figures 536–542.

Taxonomic Reference: Huber, 1969.

Species/Genera Examined: 6/5 (*Aspidistra, Campylandra, Gonioscypha, Rohdea, Tupistra*).

POLLEN TYPE: *aperture type* monosulcate (*Campylandra, Rohdea*) to inaperturate (*Aspidistra, Tupistra*); the situation in *Gonioscypha* is unclear. The aperture in *Campylandra* appears to be operculate; *polarity* heteropolar to isopolar or apolar (*Aspidistra*). POLLEN SHAPE boat-shaped-oblong to -elliptic or spherical (*Aspidistra*); *symmetry* bilateral to radiosymmetric (*Aspidistra*). POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 43 μm, range 36 (*Gonioscypha*)–48 (*Aspidistra*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate, with minute punctate-foveolae and typical foveolae intermixed (*Campylandra, Rohdea*), to openly reticulate (*Gonioscypha*), to densely gemmulate (*Aspidistra, Tupistra*); *apertural exine* not clearly seen.

REMARKS: Hutchinson (1973) specified *Rohdea* and *Tupistra* as most closely allied to Araceae. Erdtman (1952) and Ma & Hong (1990) characterized pollen of *Tupistra* as monosulcate; if so, the aperture must be obscure. Pollen of *Tupistra* and *Aspidistra* is very similar, as also that of *Rohdea* and *Campylandra*; pollen of *Gonioscy-*

pha stands apart and is somewhat reminiscent of that of Stemonaceae (pers. obs.).

Specimens Examined: Aspidistra lurida Ker Gawler (**PS-63**), *Pereira 70* (MASS), cult. Portugal. *Campylandra aurantiaca* Baker (**P-3326**), *Gould 307* (K), Bhutan. *Gonioscypha eucomoides* Baker (**P-3328**), *Brown s.n.* (K), cult. England (orig. E. Himalayas). *Rohdea japonica* Roth (**P-4611**), *Herb. Hookerianum 1867* (K), cult. *Tupistra grandis* Ridley (**P-3323**), *Anonymous s.n.* (K), cult. K (Acc. No. 181-03; orig. Penang). *T. violacea* Ridley (P-3324), *Put 1271* (K), Siam [Thailand].

Family: Cyanastraceae Figures 543, 544.

Species/Genera Examined: 1/1 (*Cyanastrum*).

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 32 μm. EXINE SCULPTURING: *nonapertural exine* retirugulate, the muri psilate; *apertural exine* not seen.

Specimen Examined: Cyanastrum johnstonii Baker (**P-3216**), *Malaisse 6072* (K), Congo.

Family: Taccaceae Figure 545.

Taxonomic Reference: Drenth, 1972.

Species/Genera Examined: 2/1 (*Tacca*).

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized to large; mean 52 μm (*T. leontopetaloides*; pollen of *T. plantaginea* averages 46 μm as calculated from SEM micrographs). EXINE SCULPTURING: *nonapertural exine* fossulate to retirugulate, minutely punctate; *apertural exine* not seen.

REMARKS: *T. plantaginea* has in the past been included in a separate monotypic genus, *Schizocapsa*. Palynologically, it is quite similar to *T. leontopetaloides*.

Specimens Examined: Tacca leontopetaloides (L.) Kuntze (**P-4228**), *Bierhorst F47* (MASS), Fiji. *T. plantaginea* (Hance) Drenth (P-4227), *Cross s.n.* (MASS), cult. Massachusetts.

Family: Pontederiaceae Figures 546–550.

Species/Genera Examined: 3/3 (*Heteranthera, Pontederia, Eichhornia*).

POLLEN TYPE: *aperture type* diaperturate, with elongate apertures (*Pontederia, Eichhornia*); pollen of *Heteranthera* is perhaps monosulcate; see "Remarks"; *polarity* subisopolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized to large; mean 46 μm, range 36 (*Pontederia*)–59 (*Eichhornia*) μm. EXINE SCULPTURING: *nonapertural exine* densely verrucate or verruculate to subrugulate (*Pontederia*); *apertural exine* not well seen.

REMARKS: The genera chosen represent all three subfamilies of Pontederiaceae. *Heteranthera dubia* is sometimes assigned to the genus *Zosterella*.

According to Seshagiri Rao & Rama Rao (1961), pollen of *Eichhornia crassipes* and *Monochoria vaginalis* may be either di- or monosulcate. This duality could not be confirmed by Simpson (1987), who found pollen throughout the family to be consistently diaperturate.

Specimens Examined: Eichhornia crassipes (Martius) Solms-Laub. (**PS-473**), *Adams 72* (MASS), Georgia. *Heteranthera dubia* (Jacq.) MacMillan (**PS-475**), *Clarke s.n.* (MASS), Michigan. *Pontederia cordata* L. (**PS-474**), *Goodale et al. 64985* (MASS), Massachusetts.

Family: Philydraceae Figures 551–558.

Species/Genera Examined: 4/4 (*Helmholtzia, Orthothylax, Philydrella, Philydrum*).

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic (*Helmholtzia, Philydrum*) to -oblong (*Orthothylax*) or -elongate (*Philydrella*); *symmetry* bilateral. POLLEN-UNIT monads (see "Remarks"). POLLEN SIZE medium-sized; mean 33 μm, range 26 (*Orthothylax*)–51 (*Philydrella*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate-reticulate (*Orthothylax, Helmholtzia, Philydrella*) to retirugulate (*Philydrum*); *apertural exine* psilate where seen.

REMARKS: Pollen was occasionally observed in tetrads in both *Philydrum* and *Philydrella*. This may be of some significance, inasmuch as this phenomenon was observed only once in 103 genera of Araceae examined that normally shed pollen in monads. The tetrads of Philydraceae are exactly as one would expect tetrads of monosulcate aroid pollen to appear. Both Erdtman (1952) and Simpson (1985a) described pollen of *Philydrum* as shed in tetragonal tetrads, but this is not regularly the case. Nor is *Philydrum* unique in the family in this regard, as stated by the latter author.

Specimens Examined: Helmholtzia acorifolia F. Muell. (**P-3280**), *Blake 19727* (K), Queensland. *Orthothylax glaberrima* (Hook. f.) Skottsb. (**P-3281**), *Chcotosbey 1933* (K), cult. K. *Philydrella pygmaea* (R. Br.) Caruel (**P-3282**), *Carter 56* (K), W. Australia. *Philydrum lanuginosum* Banks (**P-3283**), *Specht 1136* (K), N. Australia.

Family: Triuridaceae Figures 559–562.

Species/Genera Examined: 4/2 (*Sciaphila, Triuris*).

POLLEN TYPE: *aperture type* monosulcate in *Sciaphila*, possibly inaperturate in *Triuris*; *polarity* heteropolar in *Sciaphila*, possibly apolar in *Triuris*. POLLEN SHAPE boat-shaped-elliptic to -oblong in *Sciaphila*, subspheroidal in *Triuris*; *symmetry* bilateral (*Sciaphila*) or radiosymmetric (*Triuris*). POLLEN-UNIT monads. POLLEN SIZE small; mean *22 μm, range 19 (*Sciaphila stemmermanniae*)–*28 (*S. aneitensis*) μm. EXINE SCULPTURING: *nonaper-*

tural exine spinulose or subpilate (*Sciaphila aneitensis*) to finely gemmate (*S. albescens*) or verrucate with rosettelike (*Triuris hyalina*) or round, flattened (*Sciaphila stemmermanniae*) verrucae; *apertural exine* apparently similar to the nonapertural exine.

REMARKS: These plants yield very meager amounts of pollen. See Sahashi et al. (1991) for SEM and TEM micrographs of pollen of *Andruris*.

Specimens Examined: Sciaphila aneitensis Hemsley (P-3284), *Green R. S. N. H. 1165* (K), New Hebrides. *S. albescens* Benth. (**P-3285**), *Sandwith 1095* (K), British Guiana [Guyana]; (P-4489), *Schultes & Cabrera 13921* (US), Colombia. *S. stemmermanniae* Fosb. & Sachet (**P-4490**), *Stemmermann 3369* (US), Caroline Islands. *Triuris hyalina* Miers (P-4492), *Schultes 6316* (US), Colombia.

Family: Aponogetonaceae Figures 563–566.

Species/Genera Examined: 4/1 (*Aponogeton*).

POLLEN TYPE: *aperture type* monosulcate or -sulcoidate or extended monosulcate in a distinctively curved fashion (*A. natans*); *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic to -oblong; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE small; mean 23 µm, range 20 (*A. echinatus*)–29 (*A. natalensis*) µm. EXINE SCULPTURING: *nonapertural exine* foveolate-reticulate to reticulate, with small brochi and broad muri, the latter spinulose; *apertural exine* similar to the nonapertural exine, but finer.

REMARKS: Only *A. junceus*, *A. natans*, *A. tenuispicatus*, and *A. desertorum* were examined with the SEM; however, light slides were made of all nine species studied. The peculiar type of extended monosulcate pollen seen in *A. natans* is very similar to that occasionally observed in *Butomus* (J. Walker, pers. comm.).

Specimens Examined: Aponogeton desertorum Zeyher ex A. Sprengel (P-3292), *Merxmuller & Geiss 30222* (K), S. W. Africa [Namibia]. *A. echinatus* Roxb. (P-4494), *Saldanha 13922* (US), India. *A. junceus* Lehm. ex Schldl. (**P-3291**), *Moll & Nel 5552* (K), Natal [S. Africa]. *A. kraussianum* Hochst. (P-4501), *Bayliss BS6985* (US), S. Africa. *A. lakhonensis* A. Camus? (P-4495), *Tuam 1723* (US), Hong Kong. *A. natalensis* Oliver (PS-4502), *Schlechter 6716* (US), Natal. *A. natans* Engl. & K. Krause? (**P-4496**), *Fosberg & Sachet 52850* (US), Ceylon [Sri Lanka]. *A. rigidifolius* H. Bruggen (P-4497), *Bremer & Bremer 835* (US), Ceylon [Sri Lanka]. *A. tenuispicatus* H. Bruggen (P-4503), *Bogner 275* (US), Madagascar.

Family: Juncaginaceae Figures 567–570.

Species/Genera Examined: 4/3 (*Lilaea, Tetroncium, Triglochin*).

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE spherical or subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 33 µm, range 24 (*Triglochin palustris*)–39 (*Tetroncium*) µm. EXINE SCULPTURING rather openly reticulate, the muri conspicuously beaded.

REMARKS: The genera are quite uniform palynologically, and hardly to be distinguished on this basis from *Potamogeton*. See also "Remarks" under Scheuchzeriaceae.

Specimens Examined: Lilaea subulata Kunth (**PS-310**), *Pringle 1368* (MASS), Mexico. *Tetroncium magellanicum* Willd. (**PS-354**), *Hooker s.n.* (A/GH), Cape Horn. *Triglochin maritima* L. (**PS-303**), *Drake s.n.* (MASS), Massachusetts. *T. palustris* L. (**PS-309**), *Pease 20168* (MASS), Quebec.

Family: Scheuchzeriaceae Figures 571, 572.

Species/Genera Examined: 1/1 (*Scheuchzeria*).

POLLEN TYPE: *aperture type* inaperturate; *polarity* apolar. POLLEN SHAPE subspheroidal; *symmetry* radiosymmetric. POLLEN-UNIT dyads. POLLEN SIZE medium-sized; mean 33 µm. Dyads: mean 47 µm. EXINE SCULPTURING reticulate, the muri narrow and rather sharply keeled, somewhat frilled, but not beaded.

REMARKS: The dyads in *Scheuchzeria* are held together by numerous exinous strands, much as are the tetrads of certain *Typha* species (see, e.g., Punt, 1976). Pollen of *Scheuchzeria* differs more from that of the Juncaginaceae (even apart from the dyads) than does pollen of *Potamogeton*.

Specimen Examined: Scheuchzeria palustris L. (**PS-311**), *Kuzniewski 235* (MASS), Silesia.

Family: Potamogetonaceae (sensu lato) Figures 573–578.

Species/Genera Examined: 4/3 (*Potamogeton, Ruppia, Zannichellia*).

POLLEN TYPE: *aperture type* inaperturate (*Potamogeton, Zannichellia*) to tritenuate (*Ruppia*); in the latter genus, quasi-aperturate areas occur at either end and along the "upper" (convex) margin; *polarity* apolar; heteropolar in *Ruppia*. POLLEN SHAPE subspheroidal; boat-shaped-elongate and curved in *Ruppia*; *symmetry* radiosymmetric; bilateral in *Ruppia*. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 38 µm, range 30 (*Potamogeton natans*)–54 (*Ruppia*) µm. EXINE SCULPTURING: *nonapertural exine* openly reticulate, with low, narrow muri; muri beaded in *Potamogeton*, very tenuous and nodose in *Zannichellia*; brochi in *Ruppia* ± hexagonal, the muri bearing flattened, minutely spinulose triangular plates at the angles; spinules alone extending onto the surface of the tenuate (apertural) areas (the hexagonal pattern still evident); *apertural exine* spinulose in *Ruppia* (see preceding).

REMARKS: Pollen of *Potamogeton* is identical in all respects with that of *Triglochin* (see also Wang, 1990). *Zannichellia* pollen is also very similar, as correctly interpreted by Schwanitz (1967) and illustrated by Guo et al. (1990) and Wang (1990), and not "spinulose" as suggested by Erdtman (1952). Pollen of *Ruppia*, though highly modified, retains the open-reticulate exine pattern basic to these genera. SEM micrographs of pollen of *Althenia* are presented in Cook & Guo (1990), and of some additional *Potamogeton* species in Jian & Wang (1991).

Specimens Examined: Potamogeton bicupulatus Fern. (**PS-308**), *Ahles 84461* (MASS), Connecticut. *P. natans* L. (**PS-304**), *Elwell 53144* (MASS), Massachusetts. *Ruppia maritima* L. (**PS-298**), *Deane s.n.* (MASS), Maine. *Zannichellia palustris* L. (**PS-299**), *Long 8507* (MASS), Pennsylvania.

Family: Butomaceae Figures 579, 580.

Species/Genera Examined: 1/1 (*Butomus*).

POLLEN TYPE: *aperture type* monosulcate; *polarity* heteropolar. POLLEN SHAPE boat-shaped-elliptic; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 29 μm. EXINE SCULPTURING: *nonapertural exine* reticulate, the brochi much reduced toward the aperture; muri psilate, frilled; *apertural exine* not observed.

Specimen Examined: Butomus umbellatus L. (**PS-294**), *Tillotson & Tirrell s.n.* (MASS), Quebec.

Family: Alismataceae Figures 581–584.

Species/Genera Examined: 2/2 (*Alisma, Sagittaria*).

POLLEN TYPE: *aperture type* forate; *polarity* apolar. POLLEN SHAPE spherical; *symmetry* radiosymmetric. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 27 μm, range 24 (*Alisma*)–30 (*Sagittaria*) μm. EXINE SCULPTURING: *nonapertural exine* spinulose (*Alisma*) to spinose (*Sagittaria*); *apertural exine* spinulose.

REMARKS: See Jian & Wang (1991) for additional SEM micrographs of Alismataceae pollen, including that of *Caldesia*.

Specimens Examined: Alisma subcordata Raf. (**PS-307**), *Putala s.n.* (MASS), Massachusetts. *Sagittaria latifolia* Willd. (**PS-302**), *Goodale et al. 66083* (MASS), Massachusetts.

Order: Piperales Figures 585–591.

Species/Genera Examined: 4/4 (Piperaceae: *Peperomia, Piper*; Saururaceae: *Anemopsis, Saururus*).

POLLEN TYPE: *aperture type* monosulcate (*Piper*) to monoulcerate (Saururaceae) or inaperturate (*Peperomia*); *polarity* heteropolar (Saururaceae, *Piper*) or apolar (*Peperomia*). POLLEN SHAPE boat-shaped-elliptic to spherical (*Peperomia*); *symmetry* bilateral (radiosymmetric in *Peperomia*). POLLEN-UNIT monads. POLLEN SIZE small; mean 13 μm, range 11 (*Peperomia*)–16 (*Piper*) μm. EXINE SCULPTURING: *nonapertural exine* foveolate (Saururaceae) to subspinulose (*Piper* cf. *nigrum*) or coarsely verrucate (*Peperomia columella*); *apertural exine* verrucate-subspinulose in *Piper* cf. *nigrum*.

REMARKS: Pollen from but a single species each in the vast genera *Piper* and *Peperomia* obviously represents an inadequate sample; however there are few guidelines as to which species ought to be selected as most primitive or most representative. For a few additional SEM micrographs of pollen of this group, see Xi (1980).

Specimens Examined: Anemopsis californica (Nutt.) Hook. (**PS-27**), *Degener 4696* (MASS), California. *Peperomia columella* Rauh & P. Hutchison (**PS-426**), *Grayum 3264* (MASS), cult. MASS. *Piper* cf. *nigrum* L. (**PS-210**), *Grayum 3267* (MASS), cult. MASS. *Saururus cernuus* L. (**PS-28**), *Curtiss 2460* (MASS), Florida.

Family: Ephedraceae Figures 592–595.

Species/Genera Examined: 1/1 (*Ephedra*).

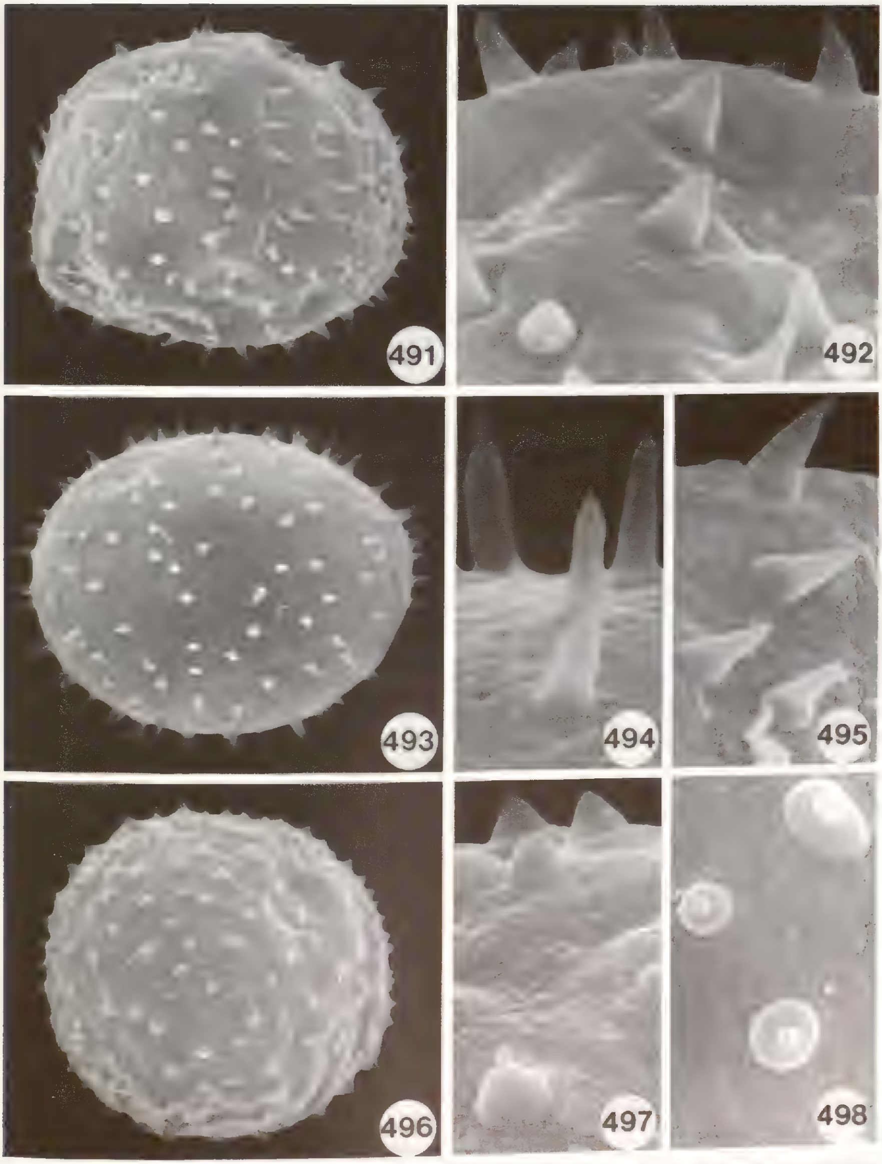
POLLEN TYPE: *aperture type* inaperturate; *polarity* isopolar. POLLEN SHAPE oblate; *symmetry* bilateral. POLLEN-UNIT monads. POLLEN SIZE medium-sized; mean 45 μm. EXINE SCULPTURING: striate, with psilate striae in the "football" pattern of *Spathiphyllum*; no columellae evident.

REMARKS: Pollen of this genus has been compared with that of *Spathiphyllum* at the TEM level by Trevisan (1980), who judged the similarities to be superficial.

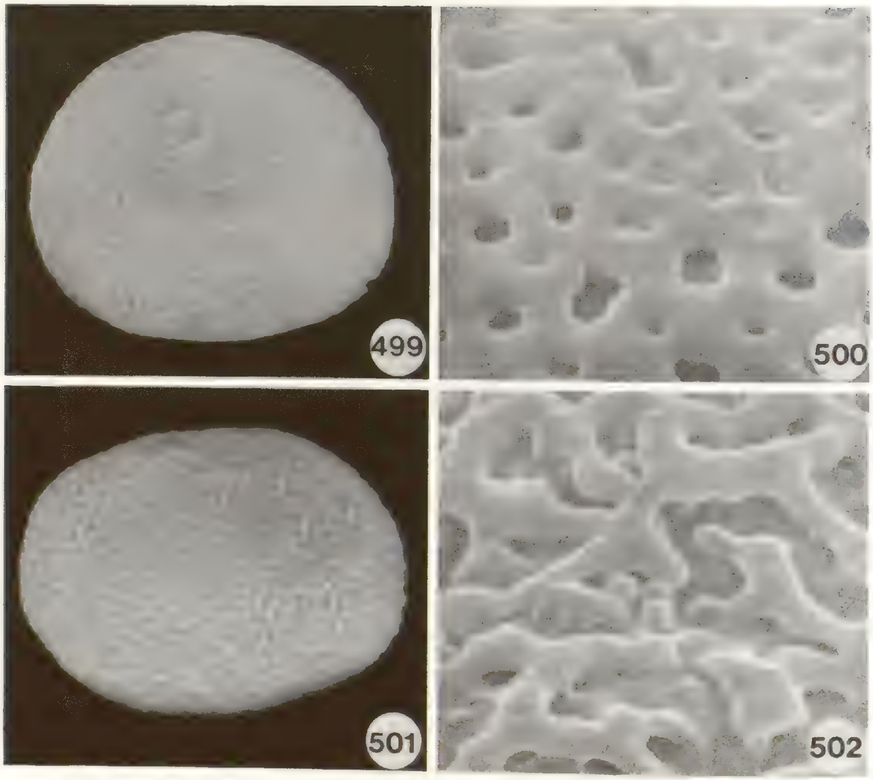
Specimen Examined: Ephedra torreyana S. Watson (**PS-443**), *Heller & Heller 3623* (MASS), New Mexico.

Discussion: Analysis of the Extrafamilial Phylogeny of the Araceae

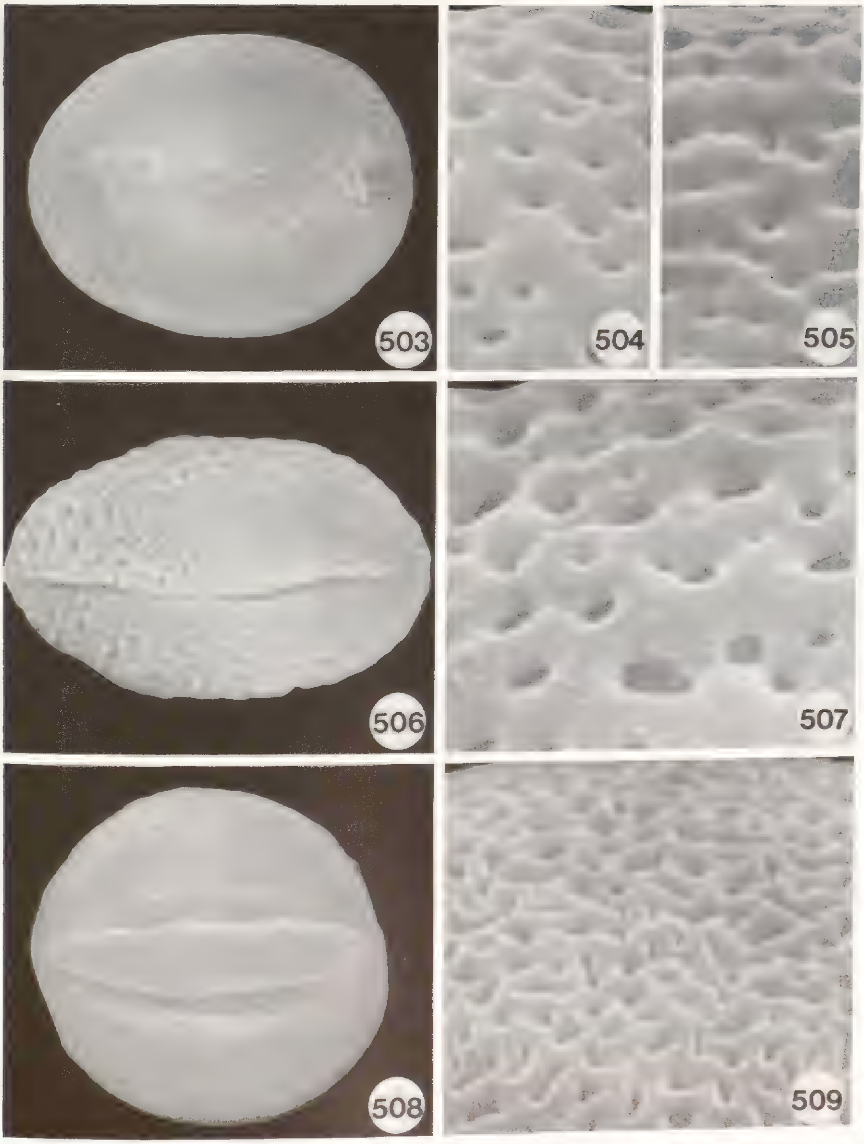
External pollen morphology sheds little light on the relationships of Araceae to other monocots. The basic, primitive type of pollen in Araceae—boat-shaped, monosulcate, small to medium-sized, with foveolate to reticulate exine sculpturing—is fairly widespread in monocots in general, occurring, in those families under consideration, in the Arecaceae (Coryphoideae and Phoenicoideae, Figs. 503–519), Cyclanthaceae (*Ludovia*, Figs. 520, 521), Cyanastraceae (Figs. 543, 544), Philydraceae (Figs. 551–558), Aponogetonaceae (Figs. 563–566), Butomaceae (Figs. 579, 580), and Piperaceae (*Piper*, Figs. 588, 589). This pollen type is generally considered primitive outside Araceae as well, in families where other types occur (see, e.g., Harley, 1990). Among these families, the Arecaceae and Cyclanthaceae show trends toward



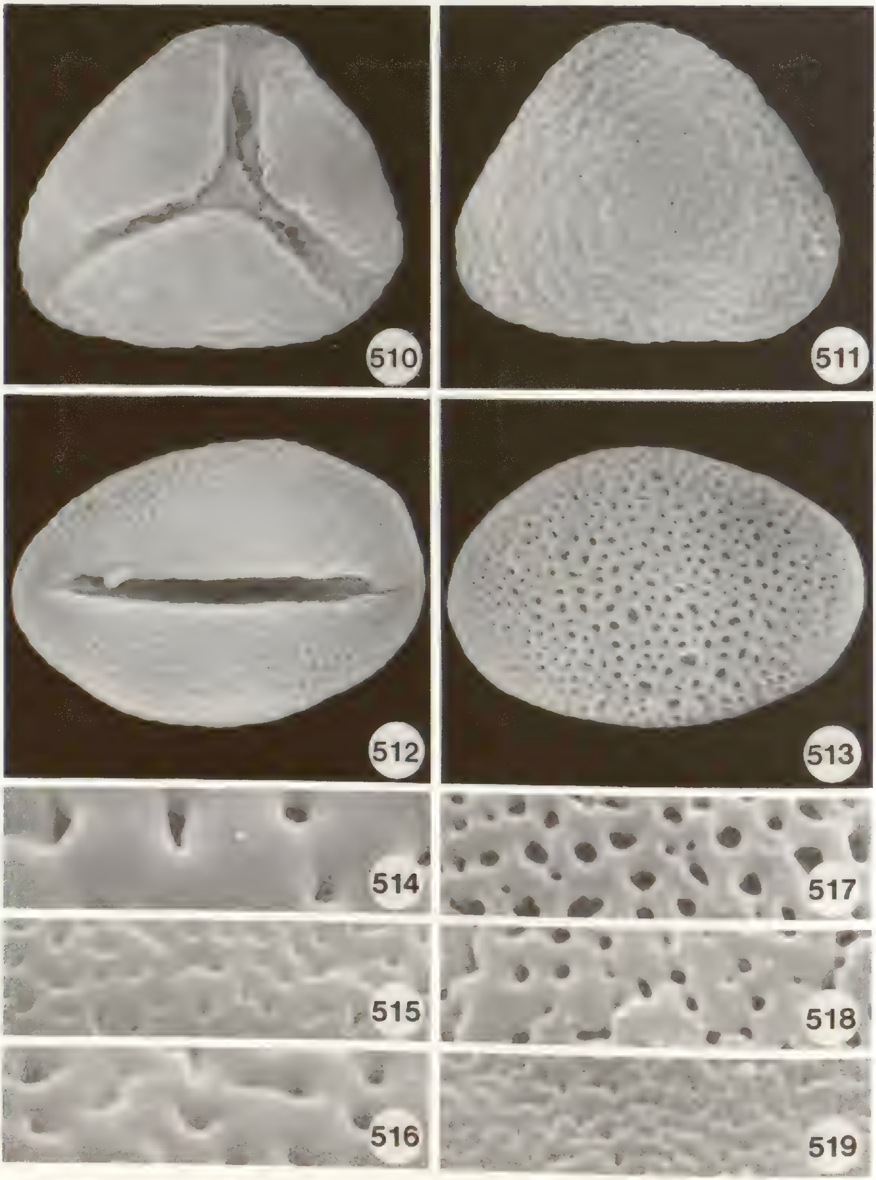
FIGURES 491–498. Pollen of Lemnaceae. 491, 492. *Spirodela punctata* (PS-258). Fig. 491, ×2,835. 493, 494. *Lemna trisulca* (PS-256). Fig. 493, ×1,910 (note aperture at 10:00). 495. *Lemna aequinoctialis* (PS-245). 496–498. *Wolffia brasiliensis* (PS-169). Fig. 496, ×2,350 (note aperture at 2:00). Fig. 497 shows the spines from an oblique aspect, Fig. 498 in a frontal view.



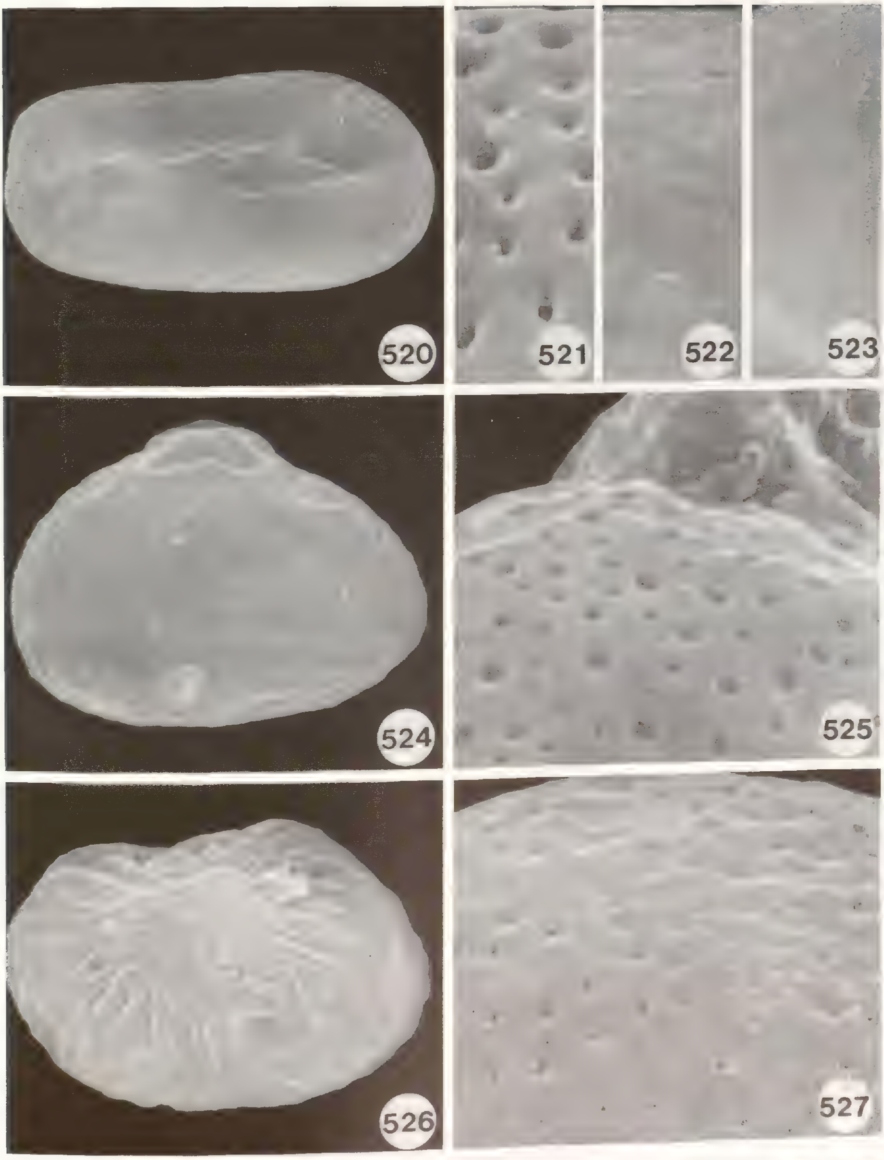
Figures 499–502. Pollen of Typhales. 499, 500. Sparganiaceae: *Sparganium eurycarpum* (PS-106). Fig. 499, ×2,020. 501, 502. Typhaceae: *Typha angustifolia* (PS-306). Fig. 501, ×2,180.



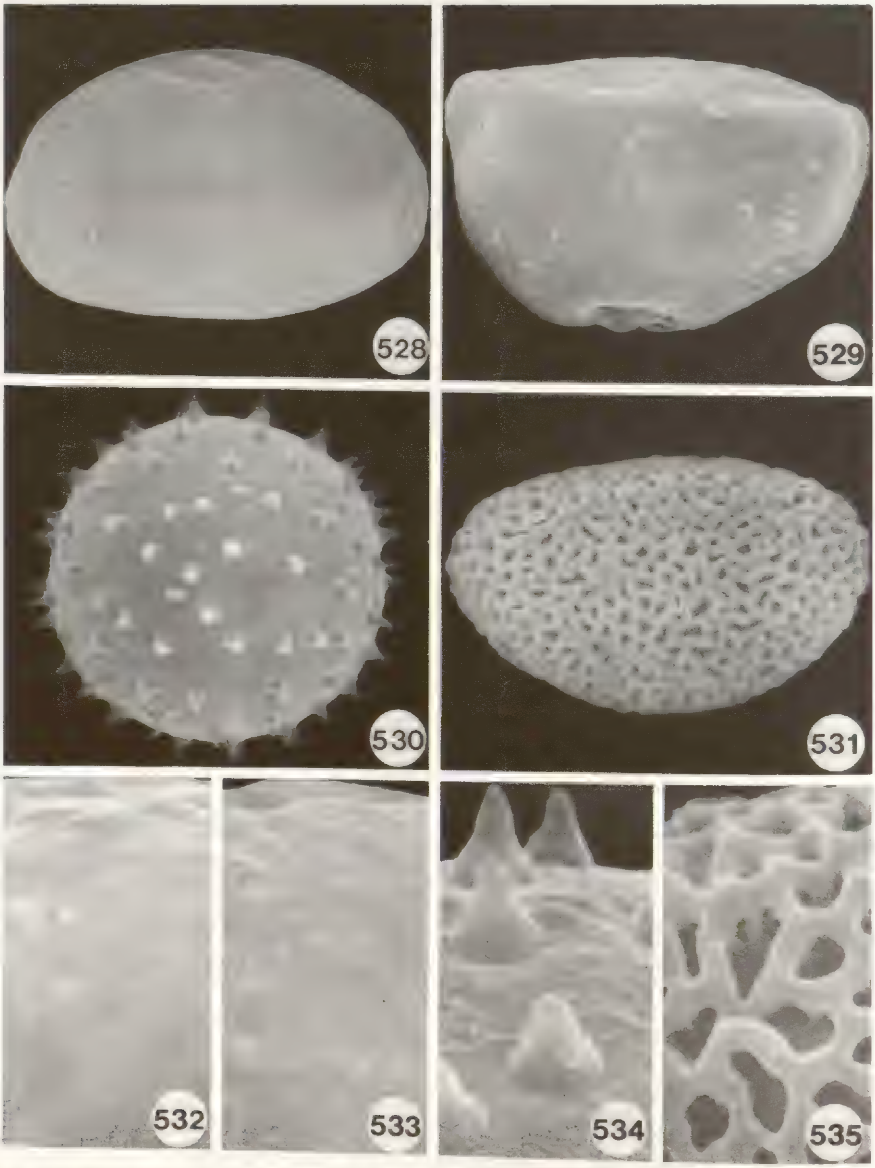
FIGURES 503–509. Pollen of Arecaceae: subfamily Coryphoideae pro parte. 503, 504. *Rhapidophyllum hystrix* (PS-344). Fig. 503, ×2,920. 505. *Trithrinax campestris* (PS-483). 506, 507. *Trachycarpus fortunei* (PS-345). Fig. 506, ×2,910. 508, 509. *Chamaerops humilis* (PS-343). Fig. 508, ×2,465.



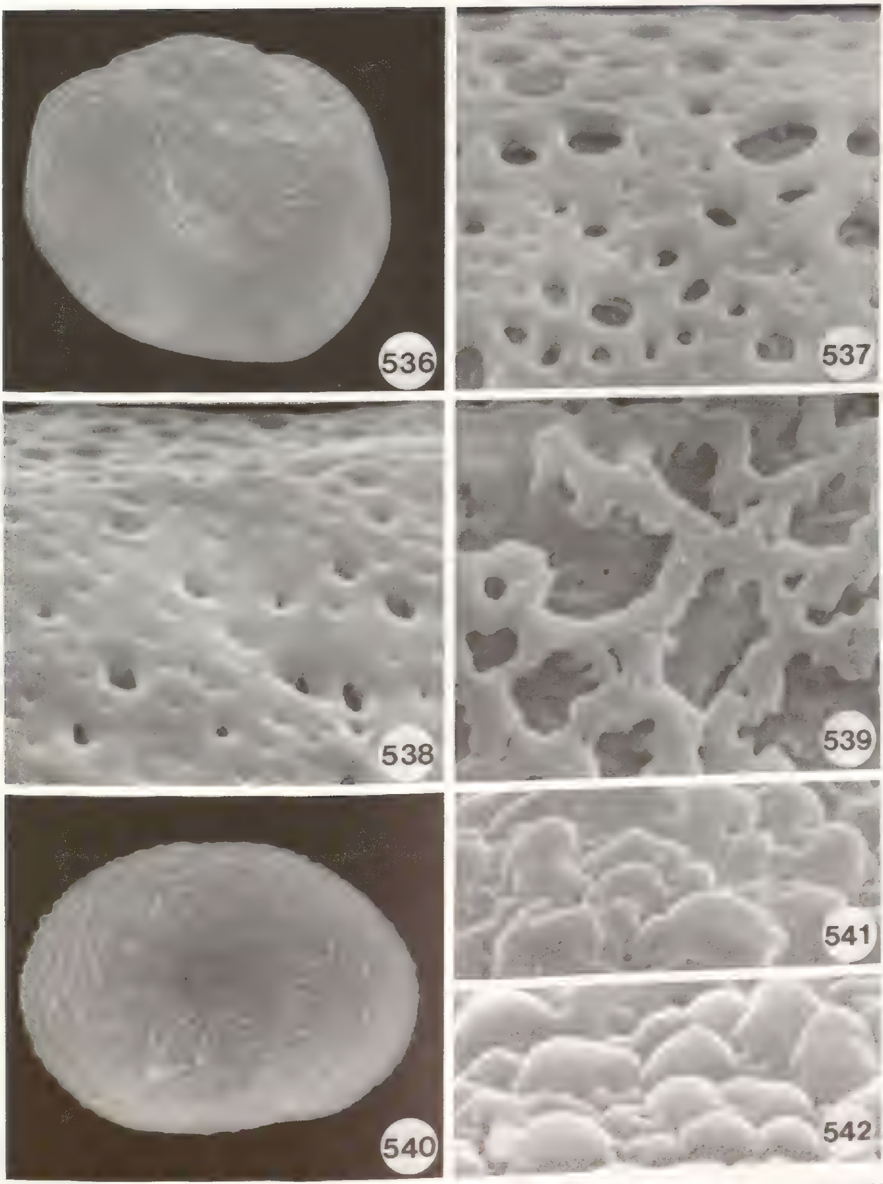
FIGURES 510–519. Pollen of Arecaceae: subfamily Coryphoideae pro parte (510, 511, 514–516) and subfamily Phoenicoideae (512, 513, 517–519). 510, 511, 514. *Cryosophila nana* (PS-346). Fig. 510 (×2,480) shows the apertural face, Fig. 511 (×2,600) the nonapertural face. 512, 513, 517. *Phoenix acaulis* (PS-348). Fig. 512 and Fig. 513 (both ×3,740) show the apertural and nonapertural face, respectively. 515. *Chelyocarpus ulei* (PS-480). 516. *Itaya amicorum* (PS-481). 518. *Phoenix hanceana* (PS-347). 519. *Phoenix dactylifera* (PS-349).



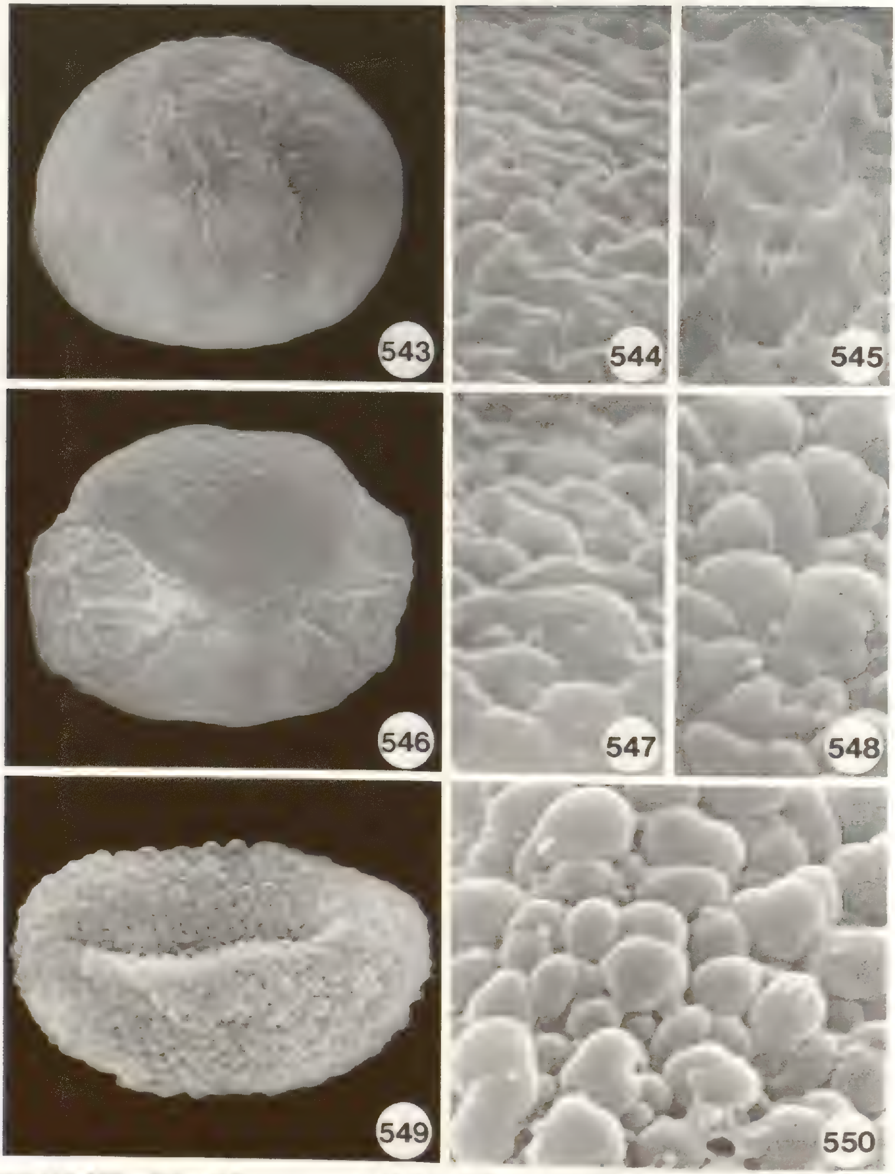
FIGURES 520–527. Pollen of Cyclanthaceae. 520, 521. *Ludovia integrifolia* (PS-108). Fig. 520, ×2,580. 522. *Chorigyne pendula* (PS-116). 523. *Evodianthus funifer* (PS-117). 524, 525. *Asplundia sleeperae* (PS-105). Fig. 524, ×3,680. 526, 527. *Cyclanthus bipartitus* (PS-432). Fig. 526, ×2,160.



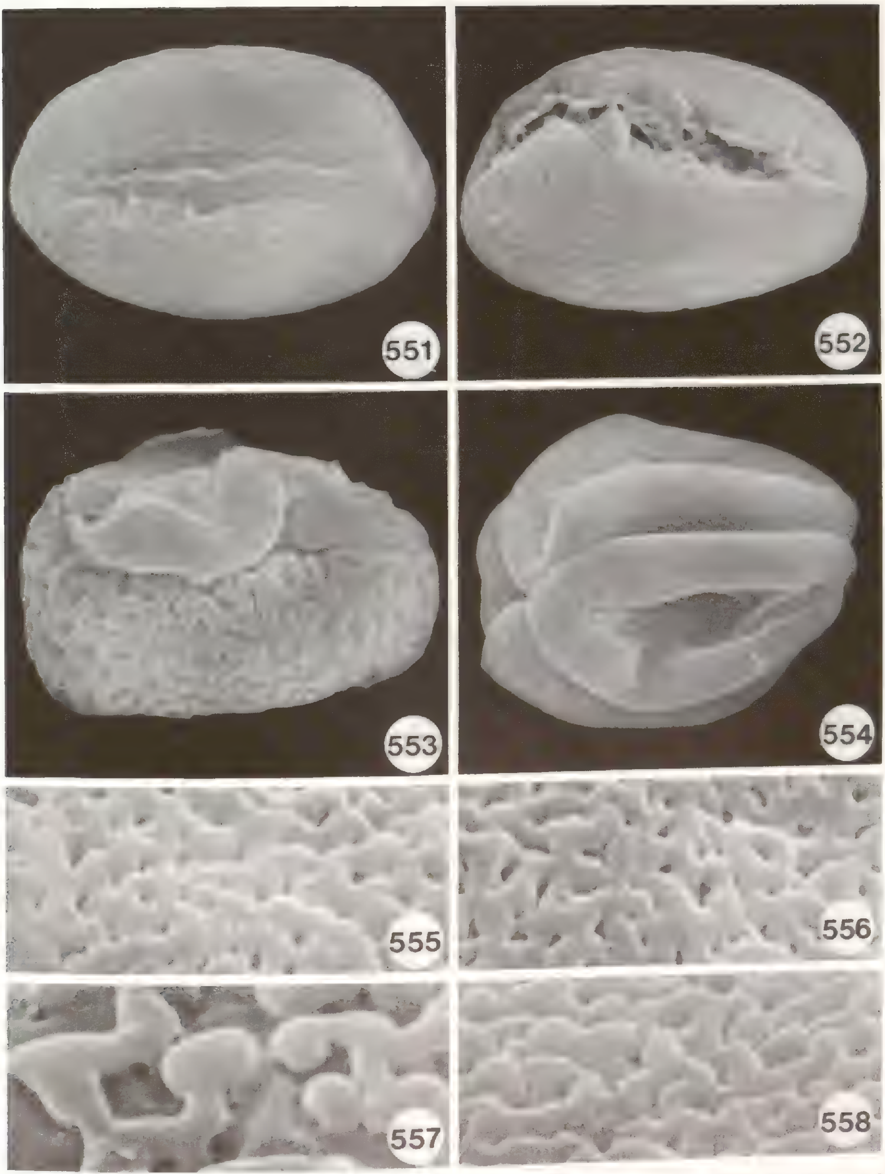
FIGURES 528–535. Pollen of Pandanaceae. 528, 532. *Freycinetia australiensis* (PS-356). Fig. 528, ×3,380. 529, 533. *Freycinetia excelsa* (PS-357). Fig. 529, ×4,175. 530, 534. *Pandanus pyriformis* (PS-476). Fig. 530, ×2,850. 531, 535. *Sararanga sinuosa* (PS-355). Fig. 531, ×3,690.



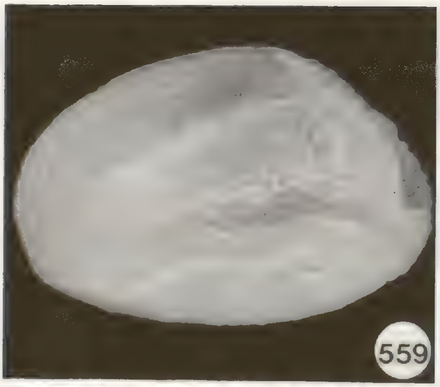
FIGURES 536–542. Pollen of tribe Aspidistreae (Convallariaceae). 536, 537. *Rohdea japonica* (P-4611). Fig. 536, ×1,580. 538. *Campylandra aurantiaca* (P-3326). 539. *Gonioscypha eucomoides* (P-3328). 540, 541. *Tupistra grandis* (P-3323). Fig. 540, ×1,930. 542. *Aspidistra lurida* (PS-63).



Figures 543–550. Pollen of Cyanastraceae (543, 544), Taccaceae (545), and Pontederiaceae (546–550). 543, 544. *Cyanastrum johnstonii* (P-3216). Fig. 543, ×2,160. 545. *Tacca leontopetaloides* (P-4228). 546, 547. *Pontederia cordata* (PS-474). Fig. 546, ×1,745. 548. *Eichhornia crassipes* (PS-473). 549, 550. *Heteranthera dubia* (PS-475). Fig. 549, ×1,380.



FIGURES 551–558. Pollen of Philydraceae. 551, 555. *Helmholtzia acorifolia* (P-3280). Fig. 551, ×2,590. 552, 556. *Orthothylax glaberrimus* (P-3281). Fig. 552, ×2,670. 553, 557. *Philydrum lanuginosum* (P-3283). Fig. 553, ×2,090. 554, 558. *Philydrella pygmaea* (P-3282). Fig. 554 (tetrad), ×1,160.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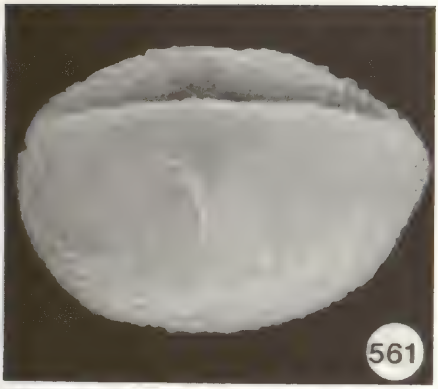
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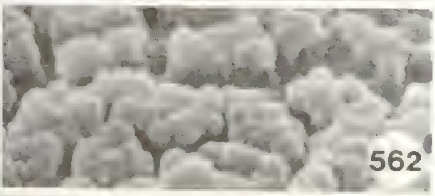
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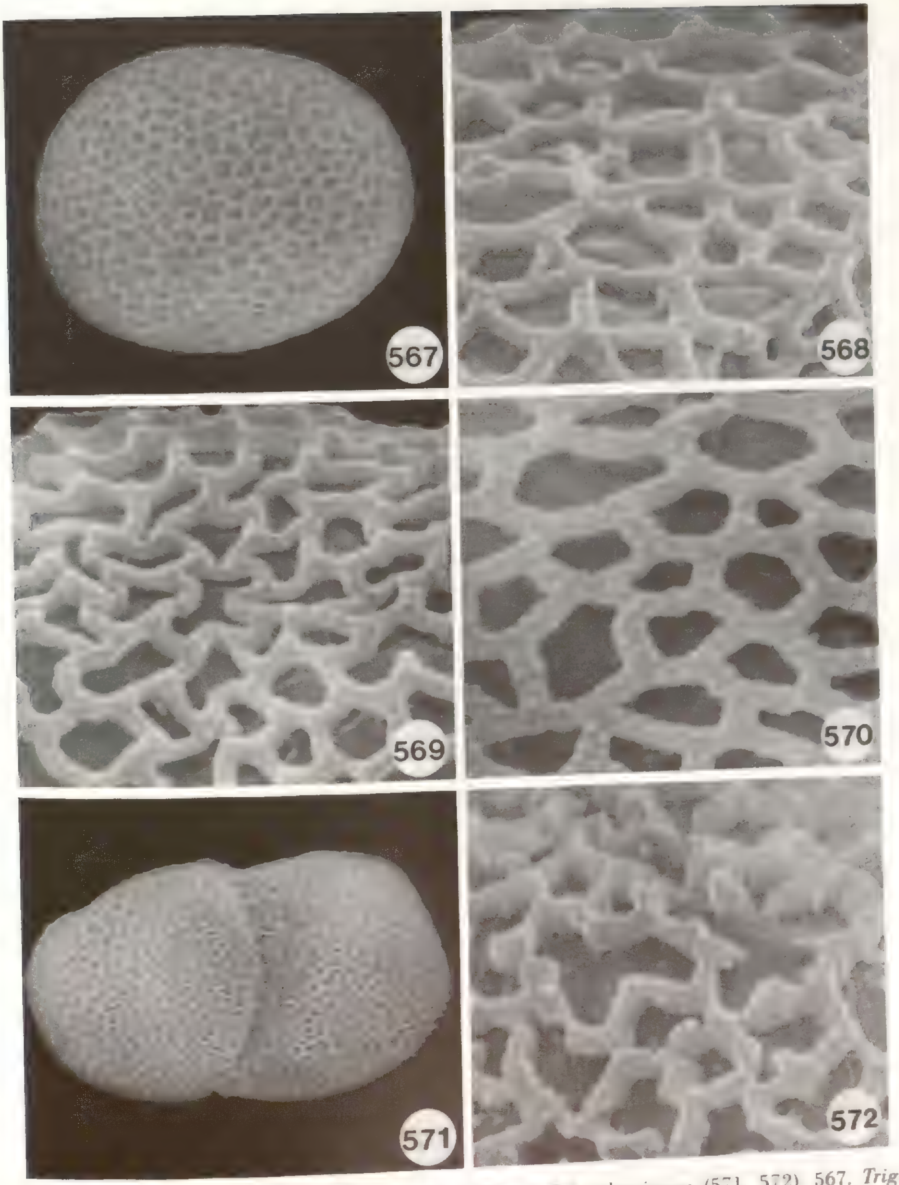
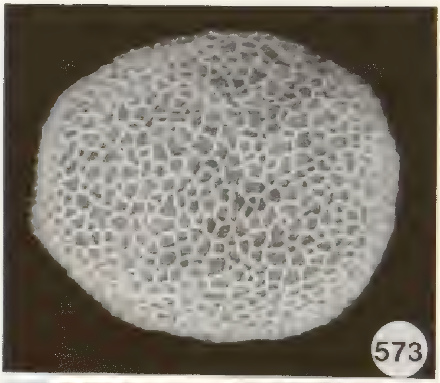
FIGURES 559–566. Pollen of Triuridaceae (559–562) and Aponogetonaceae (563–566). 559, 560. *Sciaphila stemmermanniae* (P-4490). Fig. 559, ×3,000. 561, 562. *Sciaphila albescens* (P-3285). Fig. 561, ×2,610. 563, 564. *Aponogeton junceus* (P-3291). Fig. 563, ×3,180. 565, 566. *Aponogeton natans* (P-4496). Fig. 565, ×3,060.



FIGURES 567–572. Pollen of Juncaginaceae (567–570) and Scheuchzeriaceae (571, 572). 567. *Triglochin palustris* (PS-309). ×2,330. 568. *Triglochin maritima* (PS-303). 569. *Tetroncium magellanicum* (PS-354). 570. *Lilaea subulata* (PS-310). 571, 572. *Scheuchzeria palustris* (PS-311). Fig. 571 (dyad), ×1,740.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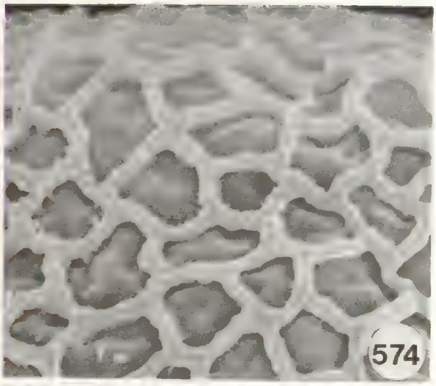
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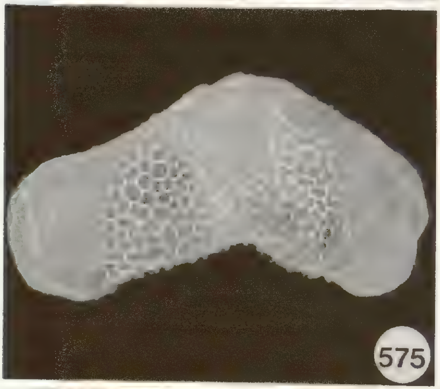
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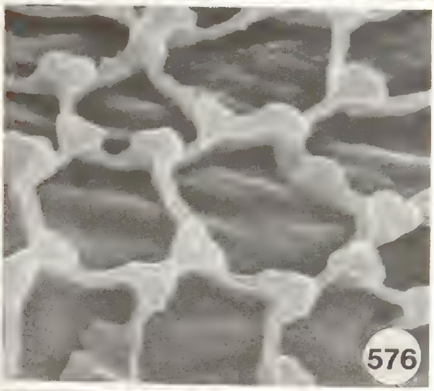
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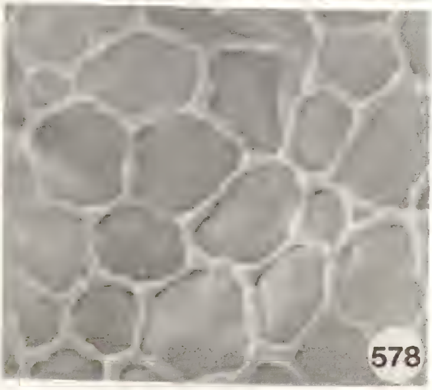
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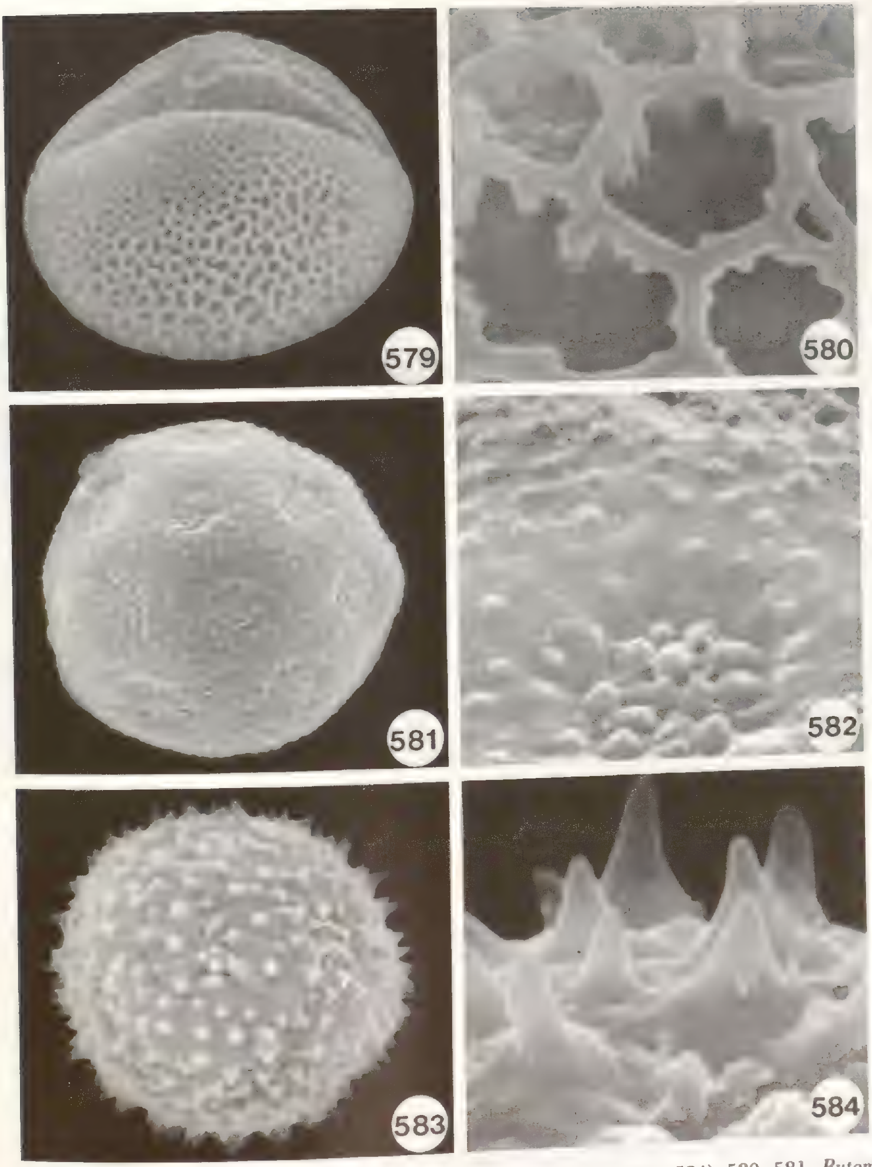
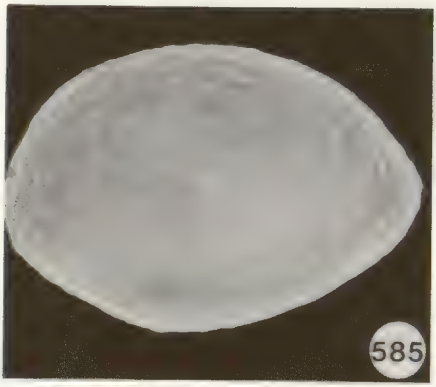
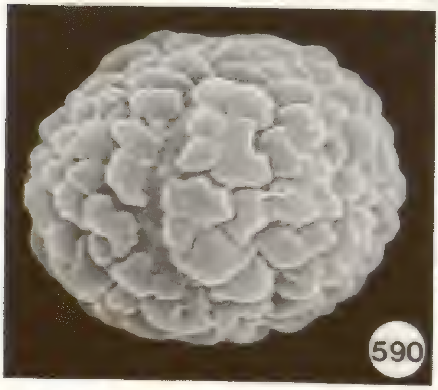
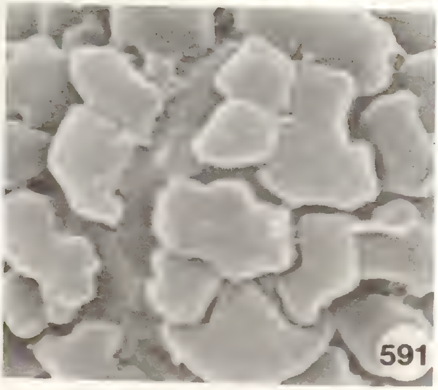
FIGURES 573–578. Pollen of Potamogetonaceae (sensu lato). 573. *Potamogeton natans* (PS-304). ×3,030. 574. *Potamogeton bicupulatus* (PS-308). 575, 576. *Ruppia maritima* (PS-298). Fig. 575, ×1,320. 577, 578. *Zannichellia palustris* (PS-299). Fig. 577, ×2,420.



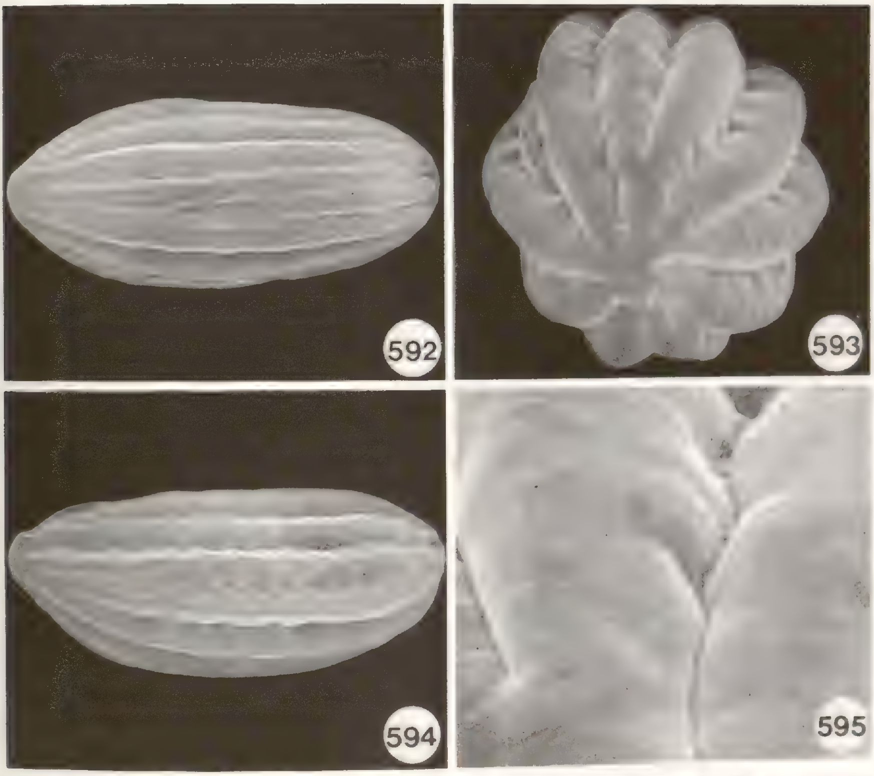
Figures 579–584. Pollen of Butomaceae (579, 580) and Alismataceae (581–584). 580, 581. *Butomus umbellatus* (PS-294). Fig. 579, ×2,295. 581, 582. *Alisma subcordata* (PS-307). Fig. 581, ×2,670. 583, 584. *Sagittaria latifolia* (PS-302). Fig. 583, ×2,370.







FIGURES 585–591. Pollen of Saururaceae (585–587) and Piperaceae (588–591). 585, 586. *Saururus cernuus* (PS-28). Fig. 585, ×6,280. 587. *Anemopsis californica* (PS-27). 588, 589. *Piper* cf. *nigrum* (PS-210). Fig. 588, ×4,870. 590, 591. *Peperomia columella* (PS-426). Fig. 590, ×6,060.



FIGURES 592–595. Pollen of Ephedraceae. 592–595. *Ephedra torreyana* (PS-443). Fig. 592 (×1,690) and Fig. 594 (×1,770) are side views of two different grains. Fig. 593 (×3,021) is an end view.

diaperturate (and in the former, zonate) pollen, as seen in Araceae. Both, however, also show strong trends toward ulcerate pollen, which is unknown in Araceae. Inaperturate pollen, which is widespread in Araceae, is totally unknown in these families as well as in the remainder of the above families, with the exception of Piperaceae. The coryphoid palms (Figs. 503, 508) and the family Philydraceae (Fig. 551) tend to have operculate pollen, which is unknown in Araceae, and the former group also shows a tendency toward trichotomosulcate pollen (Fig. 510), likewise unknown in Araceae.

Some groups generally considered very closely related to Araceae, e.g., the Lemnaceae (Figs. 491–498) and Typhales (Figs. 499–502), have pollen types (ulcerate, in both of these) that are unknown in Araceae and are far removed from the primitive condition. Thus external pollen morphology does not point clearly to any particular monocot family as the closest relative of the Araceae.

Significant observations may be made from the outgroup pollen micrographs, however, that do not relate directly to Araceae. Pollen morphology does not refute the generally accepted alliance of Sparganiaceae with Typhaceae (see Figs. 499–502). The general overall resemblance of Cyclanthaceae (Figs. 520–527) with *Freycinetia* (Figs. 528, 529, 532, 533) of the Pandanaceae, previously discussed by Harling (1958), is reflected in pollen morphology as well. Within the Aspidistreae, pollen morphology suggests a close relationship of *Aspidistra* (Fig. 542) and *Tupistra* (Figs. 540, 541), on one hand, and *Rohdea* (Figs. 536, 537) and *Campylandra* (Fig. 538), on the other hand. *Gonioscypha* (Fig. 539) appears rather different palynologically from either of these groups.

Exine sculpturing and other features provide a striking vindication of the naturalness of the order Zosterales (sensu Dahlgren & Clifford, 1982), at least, of those members with fixiform pollen. All are characterized by inaperturate pollen with open-reticulate exine and nodose muri. Pollen of *Triglochin* (Figs. 567, 568), *Tetroncium* (Fig. 569), and *Lilaea* (Fig. 570) is virtually identical, appearing to support the inclusion of all three genera in a single family, Juncaginaceae. More surprisingly, the pollen of the two *Potamogeton* species examined (Figs. 573, 574) is also nearly indistinguishable from that of the Juncaginaceae. Pollen of *Zannichellia* (Figs. 577, 578), though with a thinner and more tenuous exine, exhibits all of the same critical details. Pollen of *Ruppia* (Figs. 575, 576) is highly specialized in terms of its shape and quasi-aperturate condition; however, it retains the open reticulum characteristic of the other members of this group. *Scheuchzeria* also stands out somewhat, not only in producing pollen in dyads (Fig. 571), but also in its somewhat different exine sculpturing (Fig. 572)—a more closed reticulum with narrow, high muri. Thus pollen morphology offers good support for the recognition of Ruppiaceae and Scheuchzeriaceae as separate families. The occurrence of dyads in *Scheuchzeria*, as well as their external ultrastructure, suggests a possible alliance of this genus with the Typhales.

A thorough appraisal of all other (nonpalynological) characters must accompany the analysis of palynological data for an accurate assessment of the relationships of Araceae to other monocot families. This is not the place for analysis of characters in all monocot families comparable to that provided for the Araceae by Grayum (1984, 1990). Such a task has already been attempted by Dahlgren & Clifford (1982). These authors organized all important phenetic data for all monocot orders, and some putatively related dicot orders, and discussed in detail the possible relationships of Araceae with what they regarded as some of the most pertinent outgroups (the Alismatiflorae, Dioscoreales, Areciflorae, Typhales, and Piperales).

Before taking up the relationship of the Araceae to these and other taxa, a few words need to be said about the role of *Acorus* in monocot cladistics. This genus, as already established (Grayum, 1987, 1991), is so distinctive among the Araceae that it can only be considered the most cladistically primitive genus of the family. Indeed, there is no convincing evidence that *Acorus* is an aroid at all, nor even a sister group to the Araceae. The segregation of *Acorus* in its own family, Acoraceae, at once strengthens the definition of Araceae and encourages investigation into the true cladistic relationship of *Acorus*.

The Lemnaceae, likewise, must be dissociated from the Araceae. Dahlgren & Clifford (1982) considered the Lemnaceae a priori as a member of the order Arales. The evidence that this family bears no close relationship to the aroid genus *Pistia* has been put forth elsewhere (Grayum, 1984). The Lemnaceae appear to have relatively few characters that are completely out of place in Araceae, e.g., uniporate pollen (Figs. 493, 496), a utricular fruit, and a base chromosome number of $x = 10$. Still, there is no reason other than tradition to regard the two families as sister groups, although they share many embryological similarities and are probably more or less closely related. The Lemnaceae are still not well enough known phenetically, and in the meantime it is preferable that their cladistic relationships remain an open issue. The relationships of Lemnaceae were thoroughly considered by Landolt (1986), who tentatively suggested an alliance with Alismatiflorae.

The data of Dahlgren & Clifford (1982) concerning the remaining putatively related aroid outgroups are organized and presented in a concise and explicit manner, and I find no reason to disagree with their conclusion that the Araceae are most closely related to the Alismatiflorae. Certain groups of those examined in the present survey may be eliminated from consideration at the outset based on data presented by Cronquist (1981) and Dahlgren & Clifford (1982). The Aspidistreae, Cyanastraceae, Taccaceae, Pontederiaceae, and Philydraceae all differ from the Araceae in having at least one whorl of petaloid tepals. The first two groups have phytomelan in their seed coats. The Aspidistreae also contain chelidonic acid and steroidal saponins (the former absent and the latter extremely rare in Araceae), and they have a very different flavonoid profile from Araceae (Williams et al., 1981). Cyanastraceae and Philydraceae lack raphides, which are general throughout Araceae. The Taccaceae and *Rohdea* of the Aspidistreae have nuclear endosperm development, unlike Araceae. Taccaceae and Philydraceae also differ from Araceae in having a secretory type of anther tapetum; and Taccaceae and Cyanastraceae differ from Araceae by having simultaneous pollen mother-cell cytokinesis. The Aspidistreae, Taccaceae, Pontederiaceae, and Philydraceae all have introrse anther dehiscence, unlike Araceae. The last of these also has peltate (dorsifixed) anthers. Pontederiaceae and Philydraceae usually have a capsular fruit (all aroids have berries), and most members of the former family have septal nectaries (absent in Araceae). The Taccaceae differ further in having anomocytic stomata, epigynous flowers in a cymose umbel, and arillate seeds.

None of the above taxa is herein considered closely related to the Araceae, and none will be dealt with further. Only the Philydraceae have a more or less similar pollen morphology to the primitive type seen in Araceae. The Pontederiaceae are probably the least dissimilar to Araceae in the totality of characters, but they differ palynologically (Figs. 546–550), and, as will be seen, there are far better choices.

Representatives of the dicotyledonous Piperales, though frequently compared with the Araceae and bearing a sometimes striking superficial resemblance, show many significant differences as well, in particular: advanced vessel elements in the stems; absence of raphides (though calcium oxalate crystals of other types are present); constant presence of ethereal oil cells; lack of laticifers; S-type sieve-tube plastids (unknown in monocots); apical anther dehiscence; secretory anther tapetum; simultaneous pollen mother-cell cytokinesis; constant presence of perisperm; and, in *Piper*, a very different type of embryogeny.

Some apparent errors or oversights of Dahlgren & Clifford (1982) in their comparison of the Arales and Piperales need to be pointed out: they note that "stomata in both groups tend to be tetracytic"; they actually tend more frequently to be paracytic in Araceae (Pant & Kidwai, 1966). Also, although the inflorescence in both groups is a spadix, the flowers are always bracteate in Piperales but never so in the Araceae. Dahlgren & Clifford (1982) described endosperm development as cellular in both groups; I argue elsewhere (Grayum, 1991) that endosperm development in all Araceae (excluding *Acorus*) is better classed as helobial. And, although Dahlgren & Clifford stated that the Piperales do not develop "a large unicellular chalazal haustorium" in the endosperm (as do most Araceae), Raju (1961) described exactly such a condition in *Saururus*, *Houttuynia*, and *Anemopsis* of the Saururaceae. This is not to imply that this should be taken as evidence that the Araceae and Piperales are closely related; the overwhelming evidence is that they are not.

Dahlgren & Clifford's (1982) position that the Araceae are not closely related to the superorder Areciflorae appears to be well founded. All three families of this superorder differ from Araceae in possessing vessels in all organs (or at least in the roots and leaves), a different type of ptyxis, different leaf bases, latrorse anther dehiscence, and a secretory anther tapetum. So far as is known, all have strictly aperturate and binucleate, and overwhelmingly starchless, pollen—i.e., they do not exhibit the variation shown by Araceae in these characters. All three families show a strong tendency toward ulcerate pollen, and the palms toward operculate and trichotomosulcate pollen, all unknown in Araceae. In the palms (Bosch, 1947; Moore & Uhl, 1982) and Cyclanthaceae (Harling, 1958), the inflorescence is primitively branched, whereas in Araceae it is primitively spicate. The palms, especially, show many additional fundamental differences: they are mainly arborescent; possess silica bodies and tricin but are not (or are very rarely) cyanogenic (Gibbs, 1974); very rarely have distichous leaves; never develop compound stem bundles (Tomlinson, 1990); lack laticifers; have imbricate rather than valvate sepals, and a perianth with the two whorls generally differentiated into a calyx and corolla (Bosch, 1947); have gynoecia with regularly uniovulate locules, and frequently with septal nectaries (lacking in Araceae); exhibit simultaneous rather than successive pollen mother-cell cytokinesis; undergo nuclear endosperm development; and have a base chromosome number of $x = 18$ (Moore & Uhl, 1982), as opposed to $x = 7$ in Araceae.

The Pandanaceae are less well known; they lack silica, as do Araceae, but differ in lacking laticifers, and also appear to have nuclear endosperm development and a base chromosome number of $x = 30$.

The Cyclanthaceae show perhaps the closest approach to the Araceae of any Areciflorae; although differing in the ways enumerated previously, they lack silica and have several genera with distichous leaves; they also lack vessels in the stems (they have them in the leaves, however), and laticifers are present in *Cyclanthus* (Wilder & Harris, 1982), although they are of a different construction than those of Araceae. Pollen mother-cell cytokinesis in Cyclanthaceae is successive, as in Araceae, and endosperm development is helobial. Also, the locules of the ovary are multiovular and the fruit is a many-seeded berry, as in many Araceae. The base chromosome number is said to be $x = 9$–16 (Cronquist, 1981). Still, in light of prior considerations, the relationship of the Cyclanthaceae to the Araceae must be rather remote.

Dahlgren & Clifford (1982) enumerated six similarities between the Areciflorae and Ariflorae, two of which require emendation. Tetracytic stomata may occur in both groups, but the paracytic condition is most common in Araceae (Pant & Kidwai, 1966). Furthermore, "the absence of axile placentation in both groups" does not constitute a similarity, since axile placentation is frequent in and basic to the Araceae (Grayum, 1984).

The possible relationship of the Typhales to Araceae was briefly discussed by Dahlgren & Clifford (1982), who focused on the resemblances of Typhales to *Acorus* and particularly on the co-occurrence of a parasitic rust fungus on *Acorus calamus* and *Sparganium*. In spite of the latter feature and other similarities between these two taxa—leaf morphology, multinucleate anther tapetum cells, introrse anther dehiscence, apical placentation, and perisperm—this is poor evidence of a close relationship of Typhales to the Araceae, owing to the very questionable relationship of *Acorus* itself to the Araceae (Grayum, 1987).

Dahlgren & Clifford (1982) cited the following more general similarities between Araceae and the Typhales: the "superficially" similar inflorescences, presence of raphides, nonpetaloid tepals, basifixed anthers, amoeboid anther tapetum, successive pollen mother-cell cytokinesis, the rare occurrence in both groups of pollen in tetrads, and absence of silica bodies. Most of these are symplesiomorphies. The Typhales show certain other resemblances to Araceae not mentioned by Dahlgren & Clifford: distichous leaves, paracytic stomata, and helobial endosperm development. They differ significantly in having vessels in all organs, bracteate flowers, introrse (or latrorse) anther dehiscence, multinucleate anther tapetum cells, uniporate pollen, perisperm, one-seeded, dry fruits, and a base chromosome number of $x = 15$. While these differences are not as great as those separating Arecaceae and Araceae, they appear significant in comparison with the similarities shared by Araceae and the Alismatiflorae.

Dahlgren & Clifford (1982) produced a lengthy list of character states shared by Araceae and the Alismatiflorae that speaks for itself. I concur with their belief that this is the most closely related major group to the Araceae. Some of the more important resemblances are as follows. Both groups are herbaceous, lack secondary growth, lack silica bodies, have a similar type of leaf base, and have supervolute ptyxis. Intravaginal squamules, though rare in Araceae, are unique to these two taxa. Laticifers occur in both groups (*Lilaea*, *Aponogeton*, Limnocharitaceae, and Alismataceae of the Alismatiflorae). The basic inflorescence type of Araceae, a terminal, nonbracteate spike of small, perigoniate flowers, is most closely approached in the Alismatiflorae, most notably in the Zosterales. At least one genus of Alismatiflorae (*Aponogeton*) has a spathe subtending the inflorescence. Araceae and Alismatiflorae have basifixed anthers with extrorse dehiscence (the latter occurring in no other putative aroid outgroup); both taxa have amoeboid anther tapetum (also rare), usually with uninucleate tapetal cells, and successive pollen mother-cell cytokinesis; caryophyllad embryogeny occurs in both taxa (and in no other putative aroid outgroup); macropodous embryos are restricted among angiosperms as a whole to Araceae and the Alismatiflorae; and chlorophyllous embryos occur in both taxa (and in no other putative aroid outgroup).

Embryologists have long been almost unanimous in their support of a close affinity between Araceae and the Alismatiflorae (Grayum, 1991). Though the embryological similarities between the two taxa are indeed striking, the resemblance extends to most other fields, as the above list demonstrates. A few items may be added to Dahlgren & Clifford's (1982) list: distichous leaves occur in both taxa (e.g., in the Zosterales); both groups have predominantly paracytic stomata (contrary to the statement of Dahlgren & Clifford); Araceae and Alismatiflorae both possess helobial endosperm (i.e., endosperm of the "basal apparatus" type); and both groups have cyanogenic members (in the Alismatiflorae, notably Scheuchzeriaceae and Juncaginaceae).

The arguments against the proposed alignment of Araceae and the Alismatiflorae are as follows: most significantly, raphides—nearly universal in Araceae—are just as universally absent in the Alismatiflorae; yet other types of calcium oxalate crystals occur in Aponogetonaceae, Scheuchzeriaceae, and Juncaginaceae (Cronquist, 1981). Other differences include the absence of compound leaves and reticulate venation in the Alismatiflorae; the frequent presence in Alismatiflorae of apocarpous gynoecia, petaloid tepals, and capsular fruits; the absence of axile placentation in Alismatiflorae; the almost exclusive prevalence of trinucleate pollen in Alismatiflorae, binucleate pollen being known from only a few species of *Aponogeton* and *Triglochin* (Schnarf, 1939; Gardner, 1976); the rarity of the most primitive (monosulcate, boat-shaped, reticulate) pollen type in Alismatiflorae (occurring only in *Butomus* and *Aponogeton*); and the universal absence in Alismatiflorae of endosperm in ripe seeds. Most of these reflect the kinds of disparities that ought to be expected at the supraordinal level.

Probably the subgroup of Alismatiflorae most similar to Araceae is the order Zosterales. Although, in most cases, strongly modified for an aquatic existence, these plants still show many traits seen in Araceae. Gow (1913), convinced by his embryological studies of a close relationship between the two groups, remarked that "the general impression . . . is that the Aroid is a Pondweed that has taken to land." Perhaps this is carrying things a bit too far, but it is true that the members of the Zosterales, although rather different palynologically from the Araceae (Figs. 573–578; but see SEM micrograph of pollen of *Stylochaeton crassispathus* in Bogner, 1984a), do show a particularly close overall resemblance in several important vegetative and floral features. In addition to the resemblances general throughout the superorder, these features include: distichous leaves; presence of calcium oxalate crystals (in Scheuchzeriaceae and Juncaginaceae); cyanogenesis (in the latter two families); laticifers (in *Lilaea*); and small, tetramerous flowers with a valvate (at least in *Potamogeton*), nonpetaloid perigonium, borne in terminal, bractless (except in Scheuchzeriaceae) racemes. No other putatively related outgroup of Araceae has inflorescences so similar in every detail to the typical aroid spadix. Furthermore, flowers of *Potamogeton* are known to be protogynous (see, e.g., Philbrick, 1984), as in all Araceae, and a berrylike fruit apparently occurs in *Ruppia* (Dahlgren & Clifford, 1982). The gynoecium in this group tends to be more or less apocarpous, but then somewhere down the line the Araceae must have had an apocarpous ancestor.

The Araceae show somewhat fewer similarities to the "petaloid" members of the Alismatiflorae, e.g., the Alismatales and Hydrocharitales; however, this is not the place to delve into the systematics of the Alismatiflorae.

In summary, the closest living relatives of the Araceae are believed to be the Alismatiflorae, as Dahlgren & Clifford proposed in 1982, and particularly the order Zosterales. The Lemnaceae, although probably closely related in some way to the Araceae and Alismatiflorae, need to be studied more thoroughly and should not be regarded a priori as the sister group of Araceae. Other monocot groups, such as the Typhales, Cyclanthaceae, and Pontederiaceae, do not appear to be as closely related to Araceae as the Alismatiflorae but still show a certain degree of similarity, especially in embryological features. Of the taxa traditionally considered as close relatives of the Araceae, the Arecaceae seem to be a particularly poor choice for such a role.

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